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VOL. XXXIII.

PRELIMINARY EXPERIMENTS IN SEA-FLOOR PHOTOGRAPHY IN SOUTH AFRICAN WATERS.

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Division of Fisheries.

(With Plates I–VI and three Text-figures.)

(Read August 17, 1949.)

INTRODUCTION.

The taking of underwater photographs was apparently first attempted by Boutan (1) in the Mediterranean off the French Coast in 1893 by means of a camera operated by a diver. His later attempts at photographing at depths beyond the range of divers were not successful owing to the lack of a suitable light-source.

Just before the outbreak of the last war, Ewing and his associates (2) succeeded in producing an apparatus capable of photographing the sea bottom at depths down to 3½ miles in the North Atlantic. This camera was used for locating wrecks on the east coast of the United States, and by Shepherd and Emery (3) to determine the character of the sea bottom off California.

Through the kindness of Mr. Lamar Worzel of the Geology Department of the Columbia University of New York, an underwater camera was loaned to the Division of Fisheries for about four months this year, and, after a few initial failures, has been successfully used from the R.S. "Africana" at various places off the west coast. A full description of the apparatus is given below, since none appears to be available in previous papers dealing with its use.

The Apparatus.

The apparatus consists essentially of four parts: (*a*) the underwater camera and its water-tight housing, (*b*) the light-source water-tight housing, (*c*) the battery box and power switch, and (*d*) the bottom corer and switching mechanism.

Camera.

(Pls. I and III, A.)

The camera is a cylindrical box of sheet brass, the front lid of which opens and closes on a bayonet joint. This lid carries on its external side the camera lens (1), an electromagnet (2) with spring-latch (3) for cocking and release of the camera shutter, timing fitments (4) for synchronisation of the shutter opening and light-source flash, two copper contacts to the insulated electrical connections through the water-tight housing (5), the requisite connecting wires (6), a fitment for ensuring correct orientation of the camera in the housing, a perforated compartment (7) for holding calcium chloride or silica gel for the elimination of condensation fog on the inside of the glass window to the water-tight housing and the front of the camera lens, and a knurled turning knob (8) for forward movement of the film spool. The internal side of the lid carries the film spool take-off and take-on fitments. The camera takes No. 620 $2\frac{1}{4}'' \times 2\frac{1}{4}''$ film spools only, giving twelve exposures per single loading. The camera lens, which focuses by means of a helical mounting, is an "Alphax" *f*/4·5 with compur shutter having time and bulb adjustments and speed adjustments of 1/10, 1/25, 1/50, 1/100 and 1/200 sec. Lens aperture adjustments range from *f*/4·5 to *f*/16.

The rear end of the camera box has a red window for viewing the exposure serial number, and a wire handle for insertion and withdrawal of the camera box from the water-tight housing.

Plus × and Super × × panchromatic films were used in these experiments.

Water-tight Housing.

(Pls. I and II.)

This housing, made from a solid block of corrosion-resisting metal drilled out to a sliding fit for the camera box, is cylindrical in shape and has very thick walls. The front end has a circular window of plate glass slightly larger than the diameter of the camera lens, and the rear end is closed by a cover screwed down by means of eight screws on to a rubber gasket placed in a metal-walled groove to prevent flowing of the rubber under the high pressures at great depths.

The plate-glass window is seated on a narrow ridge of metal as close as possible in size to the hole in the case. The ridge, cut as flat as possible, has the window ground on to it with FFF carborundum. In sealing the window a thin layer of grease only is used between the glass and the metal ridge. The window is held in position by a retaining ring of metal screwed to the case. Slots deeper than the window are cut in this ring to allow the air to escape from the space in front of the window, as an air-bubble in this space will spoil the photograph.

The thickness of the window plate glass relative to various water depths and window diameters is calculated from the formula

$$T/r = \sqrt{\cdot 45h/S}$$

where T = thickness,
r = effective radius of window,
S = stress in window in lb./sq. inch,
h = depth of camera in the sea.

Two water-tight, insulated electrical connectors pierce the front of the case near its periphery below the window. Inside the case, two distance pins for correct orientation of the camera box in the case are placed relative to these electrical connectors.

Light-source Water-tight Housing.

(Pls. II and III, D and E.)

The light-source is a No. 5 photo-flash bulb (9) pressure protected under a glass cup (10) made from the sediment cup taken from the fuel system of a motor-car. The lip of this cup is ground to fit its seat, and a small amount of grease placed between the lip and its seat is an efficient seal. The cup is tightly held in place on its seat by means of an adjustable strip-metal clip (11) screwed to the seat, the dome of the cup being protected with a small disk of thick rubber (12). The seat is drilled centrally to a size to pass a No. 5 photo-flash bulb, and this hole is screw-threaded. On its underside the seat has a shallow flange on to which a hard rubber ring (13) is slipped. The seat also carries a semicircular shade of sheet brass for screening the flash from the camera lens. The flash-bulb socket of the bayonet type is placed in a raised, screw-threaded, circular portion (14) of the light-source mounting bar (15). The mounting bar is pierced by a single, water-tight, insulated electrical connector (16) positioned to fall centrally in the flash-bulb socket.

To load the light-source housing and make it water tight, a photo-flash bulb is placed in the bayonet socket, and the seat, with glass cup and screening shade, is screwed down to bear firmly on the hard rubber ring.

Battery Box and Power Switch.

(Pls. II and III, B and C.)

The battery box is a strong steel tube (17) of sufficient length and diameter to house four 1·5-volt torch batteries placed in series and a magnetically operated tumbler switch (C). At the closed end of the tube a metal spring makes contact with the battery base, while against the last battery at the open end is the tumbler switch, held firmly in position when the end plate of the tube or box is screwed in place by six screws. The end plate is pierced centrally by a single, water-tight, insulated electrical connector, and on its internal side carries a pin which fits into a hole in the tumbler-switch chassis—an arrangement to ensure orientation of the tumbler-switch in the battery box.

The insulated pole through the end plate is in contact with the battery via the tumbler-switch only when the rocker arm of the latter makes contact. Such contact is effected by a strong magnet (18) sliding a distance of about two and a half inches on rod guides mounted on the outside of the battery box. The circuit is broken when the magnet is towards the permanently closed end of the battery box, and made when near or at the opposite end.

Bottom Corer and Switching Mechanism.

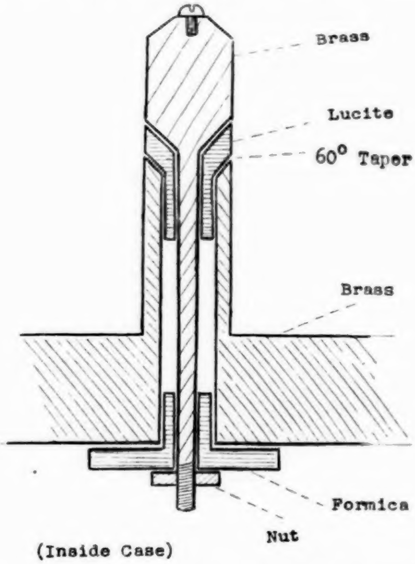
The bottom corer, a steel tube with detachable cutting edge, screws into a length of tubing which slide-fits into another length of tubing provided with a fork and bolt holes at its farther end for fixing on to a pole or staff. The inner tube is pierced to take a short length of square-section brass rod, and the outer tube has two channels about two and a half inches long cut to match the holes in the inner tube. The brass rod can therefore be passed through the inner tube to travel in the channels in the outer tube. The inner tube contains a coiled spring so placed in relation to the brass rod that the tube itself, together with the corer screwed into its lower end, is held at a distance from the pole-attachment end of the outer tube. A sharp blow on the open end of the corer will therefore cause the brass rod through the inner tube to travel two and a half inches along the channels in the outer tube towards the pole-attachment end of the outer tube, and return to its original distance position by the action of the coiled spring once the pressure of the blow is released.

Water-tight Insulated Electrical Connectors.

As these pass through the walls of housings sealed at sea-level atmospheric pressure, they have to be of special construction to remain water tight at the high pressures of great depths.

A diagram of one is given in fig. 1.

The basic feature of the design is tapering of the external insulator, so that pressure aids in making the water-tight seal. The through connection is usually made of brass, as it is a good conductor and withstands sea-water corrosion. The external insulator is made of Lucite because of its properties of plastic flow, but any other similar material may be used. Materials



(After Ewing, Maurice, Allan Vine and Worzel)

FIG. 1.

prone to fracture under pressure are not satisfactory for this tapered insulation. The internal insulator is made of some hard material such as formica.

The entire apparatus is made to withstand a pressure of 8000 lb. per sq. inch.

RIGGING THE APPARATUS.

Whether used as a free-floating or suspended unit, the various components are mounted on a long wooden pole.

In our experiments the apparatus was used as a suspended unit only, and the wooden pole consisted of a piece of teak 8 feet long by 4 inches wide by 1 inch thick.

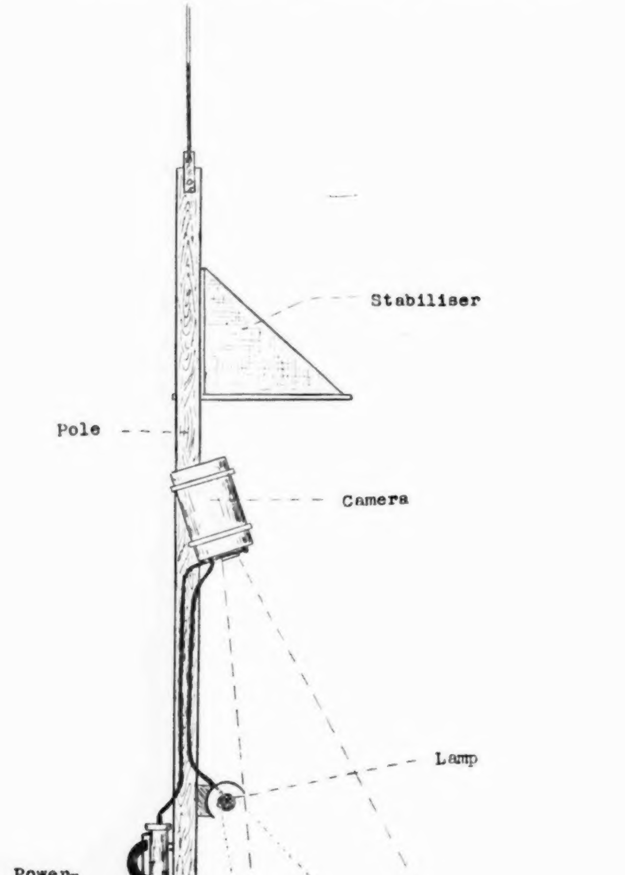


Fig. 2.

The rig is shown schematically in fig. 2.

The bottom corer and switching mechanism is bolted to the lower end of the pole, and the battery box and power switch mounted on the pole 18 inches above the lower end. The square-section brass rod of the switching mechanism is now connected to the magnet on the battery box by means of a $\frac{1}{4}$-inch round-section brass rod. The light-source water-tight housing is mounted 6 inches above the battery box, *i.e.* 2 feet from the cutting edge of the bottom corer in its normal distance position. The camera housing is mounted 5 feet above the light-source housing, *i.e.* 7 feet from the corer cutting edge, canted just sufficiently to the right (or left if desired) of the vertical to exclude the bottom edge of the pole from the field of view. Relative to the camera cant, the light-source housing is canted proportionately to ensure that the flash illuminates the entire field of view and yet is screened from the camera lens by the shade-reflector on the housing.

It will be obvious, of course, that the camera and light-source housings may be mounted on the pole at any such distances from the cutting edge of the bottom corer as will give the size of field of view and relative lighting desired. Fitted as described above, the field of view is 4 feet by 4 feet.

Connecting wires, heavy vulcanite in rubber cable or motor-car high-tension cable, are now run between the terminals on the camera housing, the light-source housing and the battery box in accordance with the wiring diagram given in fig. 3.

The exposed wires at the terminal connecting points are made water tight by wrappings consisting of two layers of para rubber tape covered by two layers of ordinary insulation tape extending for two to three inches from near the base of the terminal on to the cable.

On striking the sea-floor, the tumbler switch in the battery box makes contact by means of the magnet, current flows to the camera and activates the electromagnet, which releases the spring-latch holding the camera shutter in the cocked position. Mounted to the shutter arm is a brass contact which, as the shutter arm reaches the end of its travel, completes the circuit out of the camera to the flash bulb. The brass contact on the arm is screw adjusted, so that synchronisation between shutter opening and flash may be obtained.

For testing in air it is of course necessary to run earth wires between the components.

As a suspended camera rotates when lowered into the sea owing to the twisted lay of the stranded steel wire rope used, and also the motion through the water of the rig, producing a torque, a small stabiliser in the form of a triangular canvas sail is fitted to the pole above the camera housing. This sail has been found to slow down rotation to a negligible point.

The top end of the pole carries a metal fork with eye for attachment of the lowering wire by means of two shackles and a swivel.

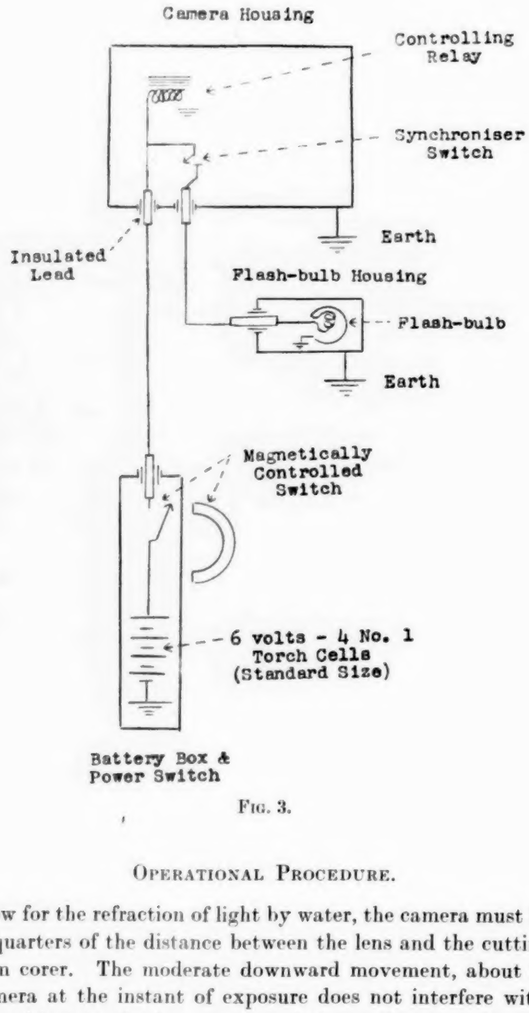
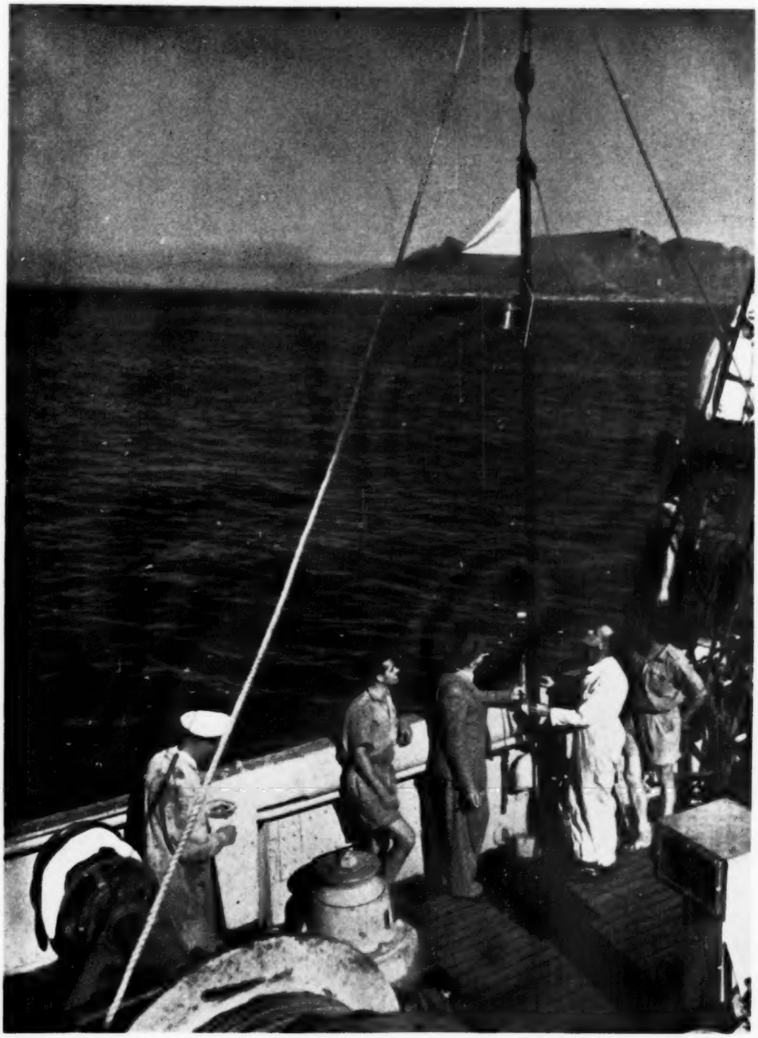


FIG. 3.

OPERATIONAL PROCEDURE.

To allow for the refraction of light by water, the camera must be focused for three-quarters of the distance between the lens and the cutting edge of the bottom corer. The moderate downward movement, about $2\frac{1}{2}$ inches, of the camera at the instant of exposure does not interfere with its performance, subject to the lens aperture being such as to give a depth of focus in excess of this distance, but even a slight rotation about the vertical axis will ruin the pictures.



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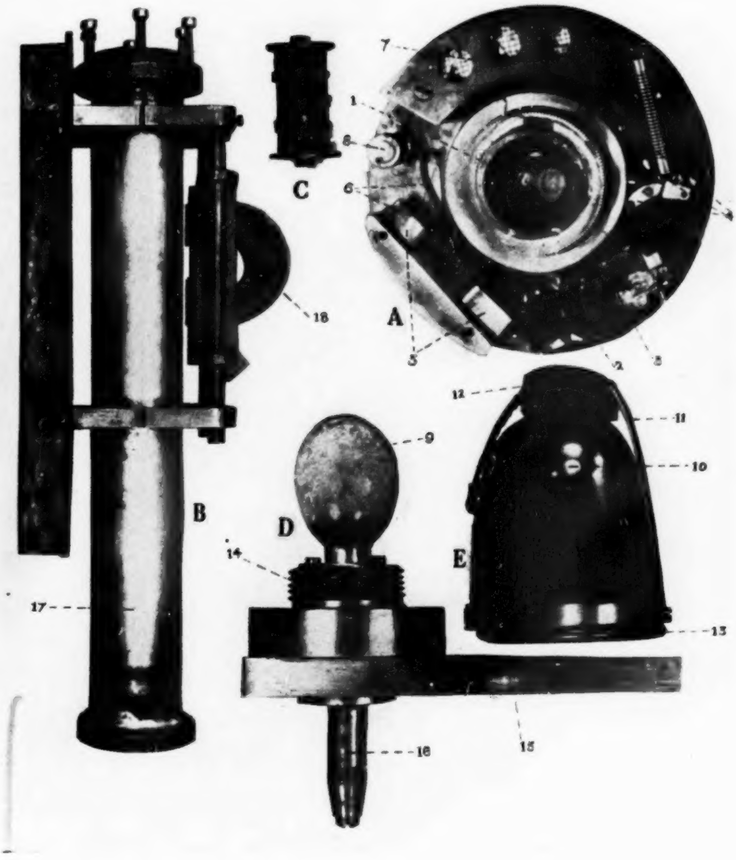
A
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C
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E
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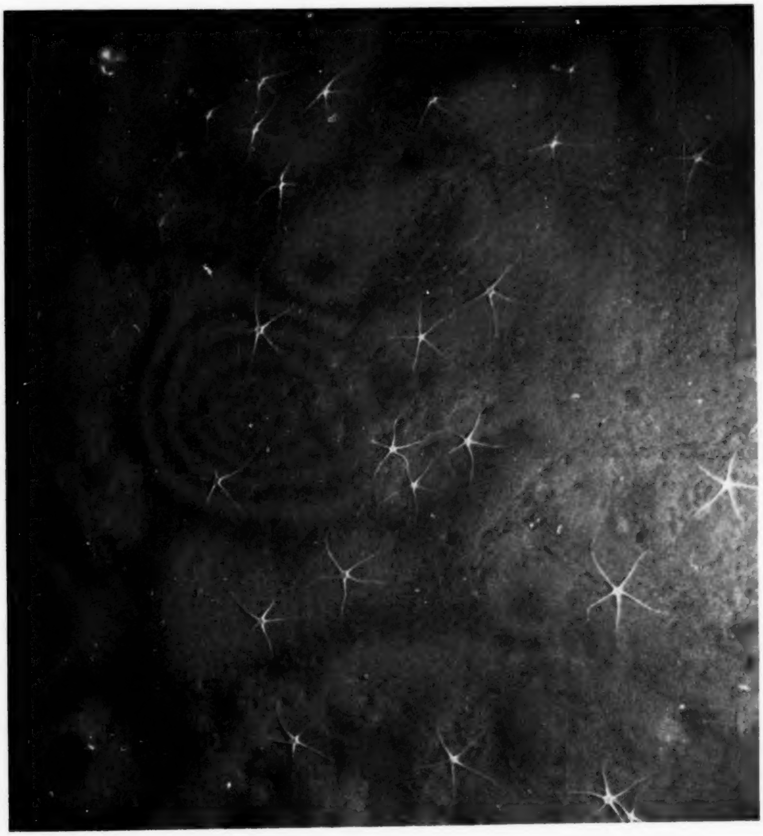
Cecil von Bonde, J. M. Marchand and S. G. Gibbons.

Neill & Co., Ltd.



Cecil von Bonde, J. M. Marchand and S. G. Gibbons. *Neill & Co., Ltd.*

Cecil von Bonde, J. M. Marchand and S. G. Gibbons. *Neill & Co., Ltd.*

Only one picture per lowering can be taken, and therefore between shots the camera must be removed from its housing for re-cocking of the shutter and forward winding of the film spool. Also a fresh flash bulb must be inserted in its housing.

Before lowering the gear over the ship's side a sounding is taken, and the gear then allowed to run out by its own weight (about 60 lb.) until a few metres off the bottom, the length of wire out being recorded by a metre sheave over which the wire runs. At this point descent is momentarily stopped with a view to eliminating rotation, and the gear is then lowered the remaining distance at a somewhat slower rate until it strikes the bottom. Considerable care and experience are necessary, especially at greater depths, to avoid excessive overrun of the wire after the bottom strike, as the gear must not be allowed to fall flat on the bottom and so endanger the components on the pole, particularly on rocky bottom.

Sea Trials.

Altogether 48 underwater exposures were made, from which 22 excellent negatives were obtained, as follows:

(i) Green Point Lighthouse, bearing 117°, distant 6·75 miles, depth 41 fathoms, sand and mud bottom—9 exposures (1/25 and 1/50 sec. at *f*/4·5 and 6·3), no definition.

(ii) North-west corner of Robben Island Lighthouse, bearing 145°, distant 2·25 miles, depth 22 fathoms, rocky bottom—3 exposures (1/25 sec. at *f*/4·5 and 6·3), no definition.

(iii) Cape Columbine, bearing 126°, distant 17·8 miles, depth 130 fathoms, dark green mud bottom—6 exposures (1/25 and 1/50 sec. at *f*/4·5, 6·3, 9 and 12), 5 excellent negatives and 1 underexposed (1/25 sec. at *f*/12).

(iv) Dassen Island Lighthouse, bearing 084°, distant 21 miles, depth 114 fathoms, green sandy mud bottom—6 exposures (1/10, 1/25 and 1/50 sec. at *f*/4·5, 6·3, 9 and 12), 5 excellent negatives and 1 underexposed (1/10 sec. at *f*/12).

(v) Dassen Island Lighthouse, bearing 066°, distant 27 miles, depth 154–165 fathoms, dark green mud bottom—6 exposures (1/25 and 1/10 sec. at *f*/4·5, 6·3 and 9), 5 excellent negatives and 1 blank (failure of synchronisation of shutter and flash).

(vi) Cape Columbine, bearing 111°, distant 71 miles, depth 220–222 fathoms, dark green mud bottom—6 exposures (1/10 and 1/25 sec. at *f*/4·5, 6·3 and 9), all excellent negatives.

(vii) Dassen Island Lighthouse bearing 072°, distant 26·5 miles, depth 145 fathoms, dark green mud bottom—1 exposure (1/10 sec. at $f/4{\cdot}5$), excellent negative.

(viii) In False Bay: (*a*) off Miller's Point, depth 17 fathoms, rocky bottom—1 exposure (1/10 sec. at $f/6{\cdot}3$), no definition; (*b*) Kogel Bay, depth 14 fathoms, rocky bottom—7 exposures (1/10 and 1/25 sec. at $f/6{\cdot}3$), no definition.

(ix) Anchorage, Table Bay, depth 6 fathoms, muddy sand bottom—3 exposures (1/25 and 1/50 sec. at $f/4{\cdot}5$), no definition.

All operations were carried out during daylight hours, except those enumerated at (iii), (vii) and (ix), which were undertaken at night ((iii) and (vii) being A.M. and (ix) being P.M.).

Discussion.

All attempts to obtain clear pictures in shallow coastal waters proved abortive.

Experiments carried out with the camera in the exhibition tanks at the Marine Biological Laboratories, Sea Point, provided conclusive proof that the shallow-water failures were occasioned by detrital matter and planktonic life in suspension in the water, causing dispersion of light to an extent precluding clear definition of the bottom and objects on it.

In relation to this finding, and judging from the fine definition of the deeper water pictures obtained, the water near the bottom in the greater depths probed during our experiments must be exceedingly free from suspended matter of any kind.

Daylight or darkness at the surface had no apparent effect on the quality of the negatives obtained.

With a No. 5 photo-flash bulb the duration of the flash is of the order of 1/70 sec., and therefore shutter speeds in excess of the flash duration speed were not used. At shutter speeds of 1/10, 1/25 and 1/50 sec., negatives of adequate density are obtained with a lens aperture as small as $f/9$, but at $f/12$ the negatives are extremely thin.

Pls. IV, V and VI are three examples of the 22 sea-bottom pictures obtained.

Pl. IV, taken in 114 fathoms 21 miles to the westward of Dassen Island, shutter speed and lens aperture being 1/10 sec. and $f/6{\cdot}3$ respectively, is typical of the sea-floor of the shallower, shorewards parts of the Dassen Island trawling grounds. The central dark object is a single, medium-sized specimen of the dark purple Heart Urchin (*Spatangus capensis*) fairly common on these grounds. Its path of progress from the top of the picture

is well defined, and in its forward movement through the mud it has shovelled mud plus small sponges on to its back. The density on these grounds of Brittle-stars (*Dictenophiura* sp.) and small globular sponges (the very numerous pebble-like objects) is remarkable. In the lower right corner is a single Hermit Crab (*Parapagurus ? dimorphus*) bearing commensal anemones on its shell.

Pl. V, taken in 165 fathoms 27 miles south-westwards of Dassen Island, shutter speed 1/10 sec. and lens aperture *f*/9, is characteristic of the central depth-range portions of the Dassen Island trawling grounds. With removal of the considerable population of Brittle-stars (*Dictenophiura* sp.) (note the mutilated individuals), and the solitary Hermit Crab (*Parapagurus ? dimorphus*) in the upper left-hand corner, the picture is reminiscent of an aerial photograph taken over sand-dune desert country.

Pl. VI, taken in 220 fathoms 71 miles north-westwards of Cape Columbine, shutter speed 1/10 sec. and lens aperture *f*/6·3, shows the nature of the sea-floor of the deeper regions of the Cape Columbine stock-fish trawling grounds. Brittle-stars (*Dictenophiura* sp.) are still present but in reduced numbers, and three Hermit Crabs (*Parapagurus ? dimorphus*), bearing commensal anemones on their shells, are seen. The noticeable streak tracks, and the finely pitted appearance of the muddy bottom, particularly clear towards the upper side of the picture, are apparently "footsteps in the sands of time" left by hermit-crabs. Here again, in the absence of the invertebrate population, the picture might be mistaken for an aerial photograph of some parts of the Namib Desert in South-West Africa.

In these instances only were fish caught within the field of view of the camera, and although in no case in very sharp focus, are identifiable in two instances as Gilchrist's Triple-fin (*Tripterophycis gilchristi*), a member of the codfish family.

Summary.

Following an introduction dealing with earlier work in submarine photography, this paper gives a description in detail of the apparatus loaned to the Division of Fisheries by the University of Columbia, in the United States of America.

The various components of this camera and their relative importance are pictorially displayed.

The operation of mounting and using the equipment is then adequately dealt with.

Sea trials covering over 40 exposures, the experiments being conducted in depths from 7 to 222 fathoms, are then described.

A short discussion on the results obtained, including names of bottom organism photographed, concludes the paper.

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(For additional literature see (2) above.)

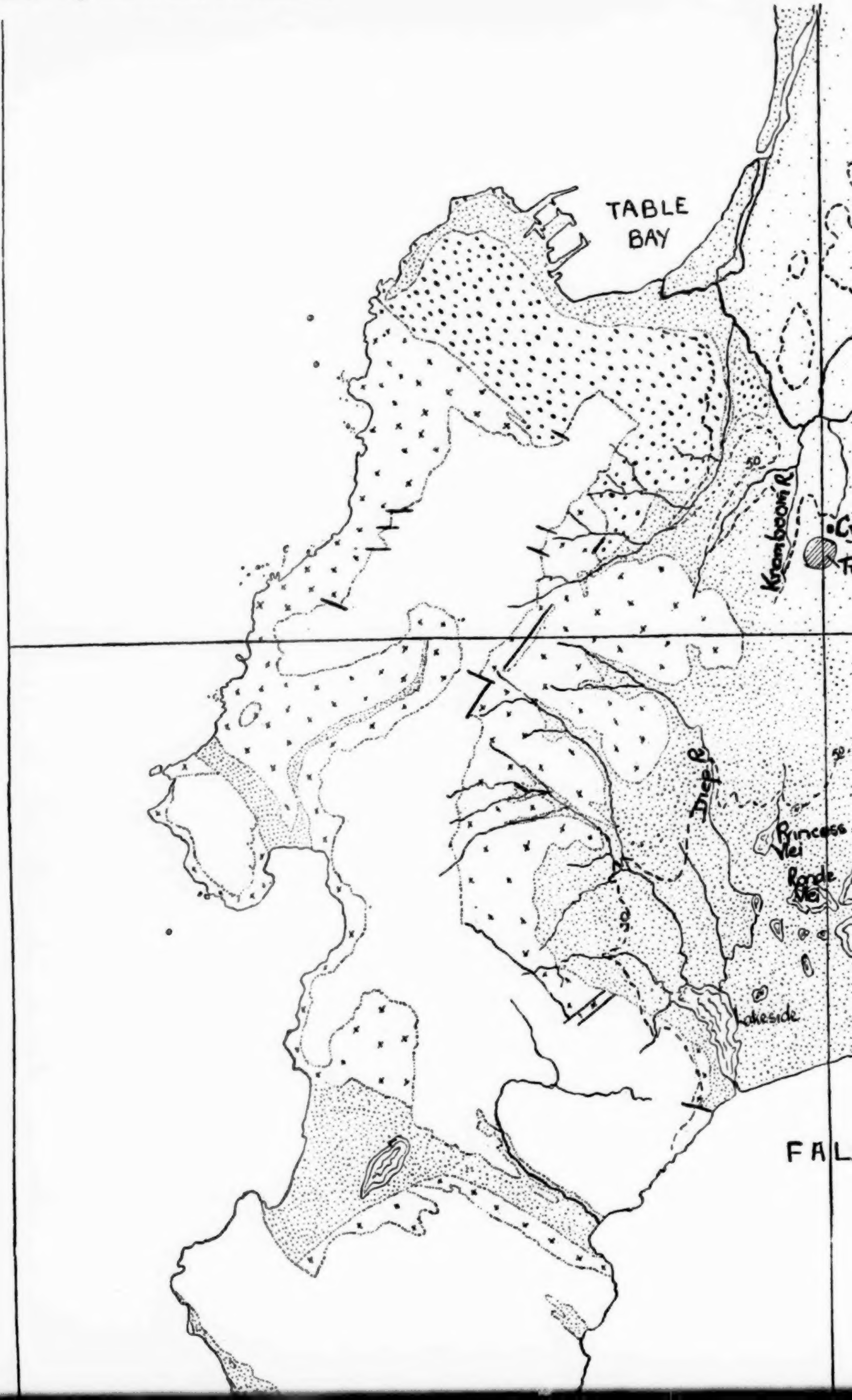
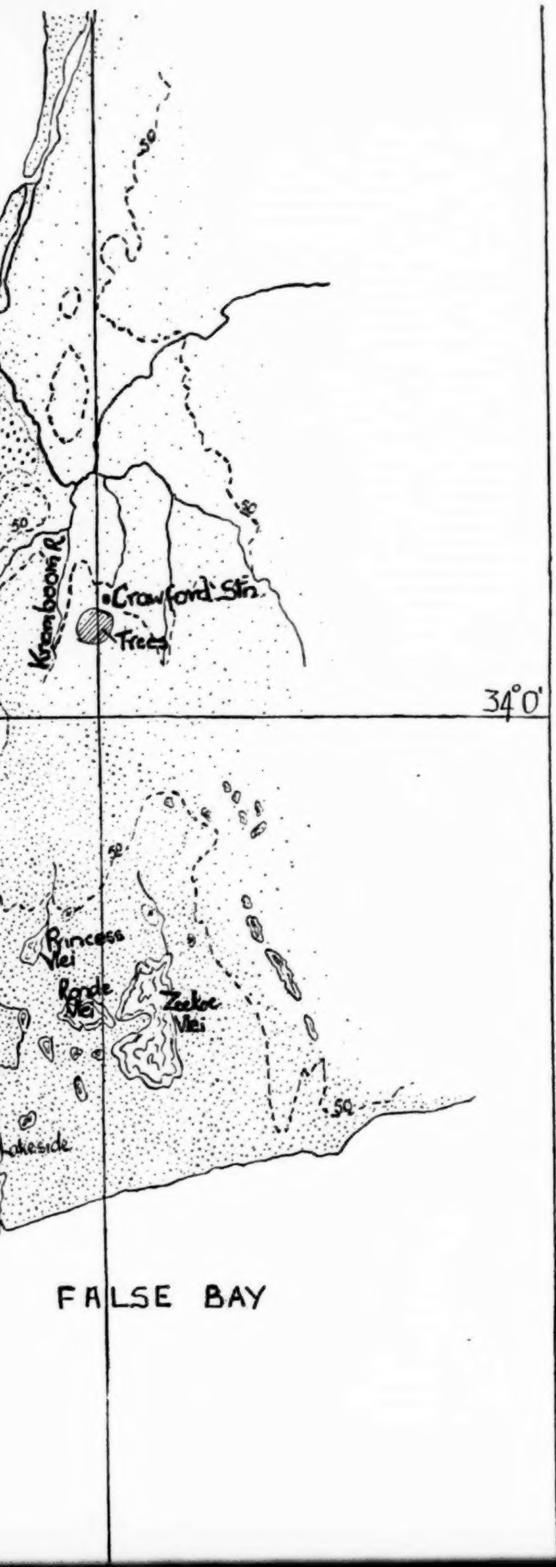


TABLE BAY
Kromboom R
Diep R
Princess Vlei
Ronde Vlei
Lakeside
FAL



Kromboom R.
Crawford Stn.
Trees
34°0'
50
Princess Vlei
Ronde Vlei
Zeekoe Vlei
Lakeside
FALSE BAY

INDEX.

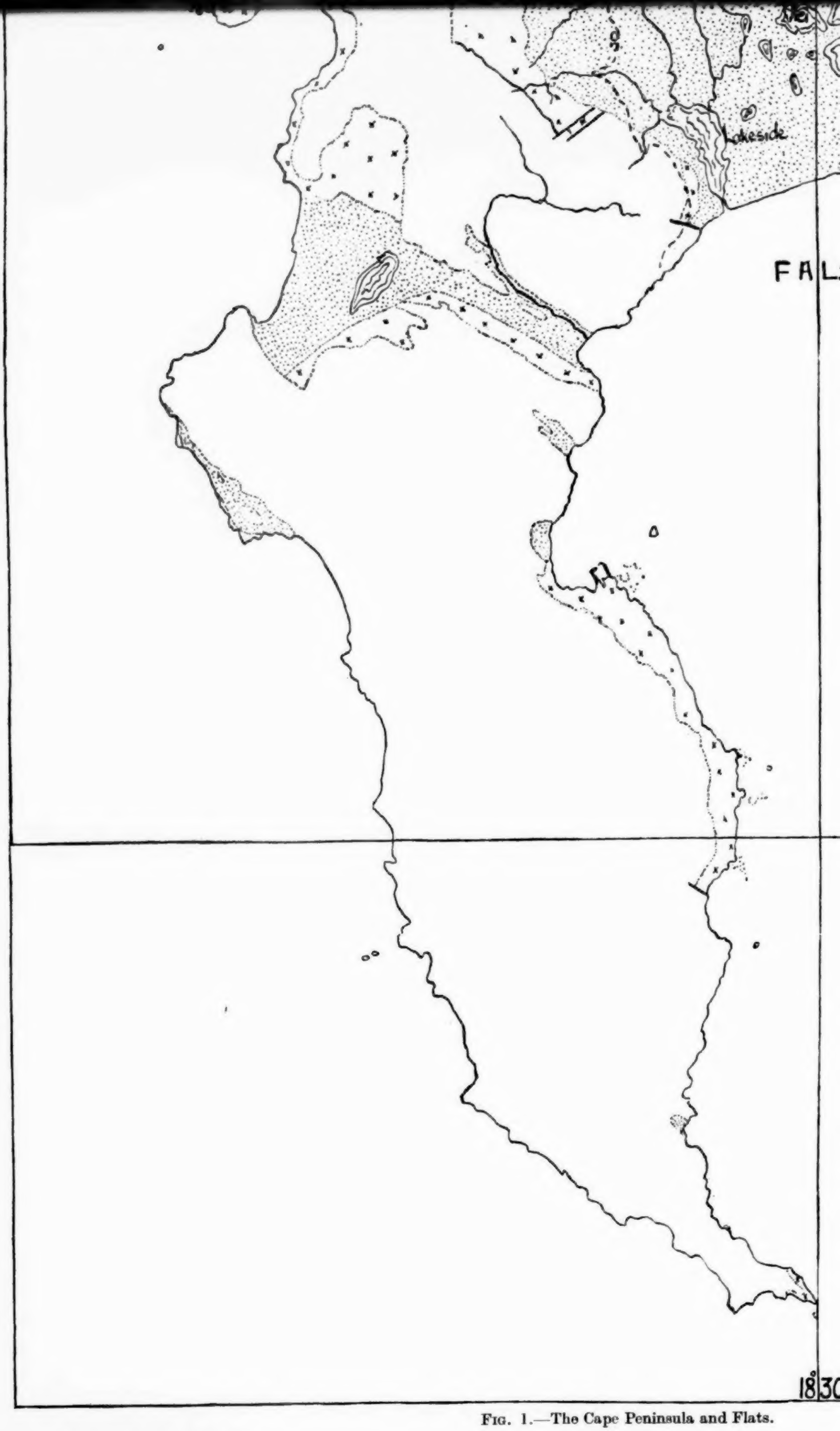
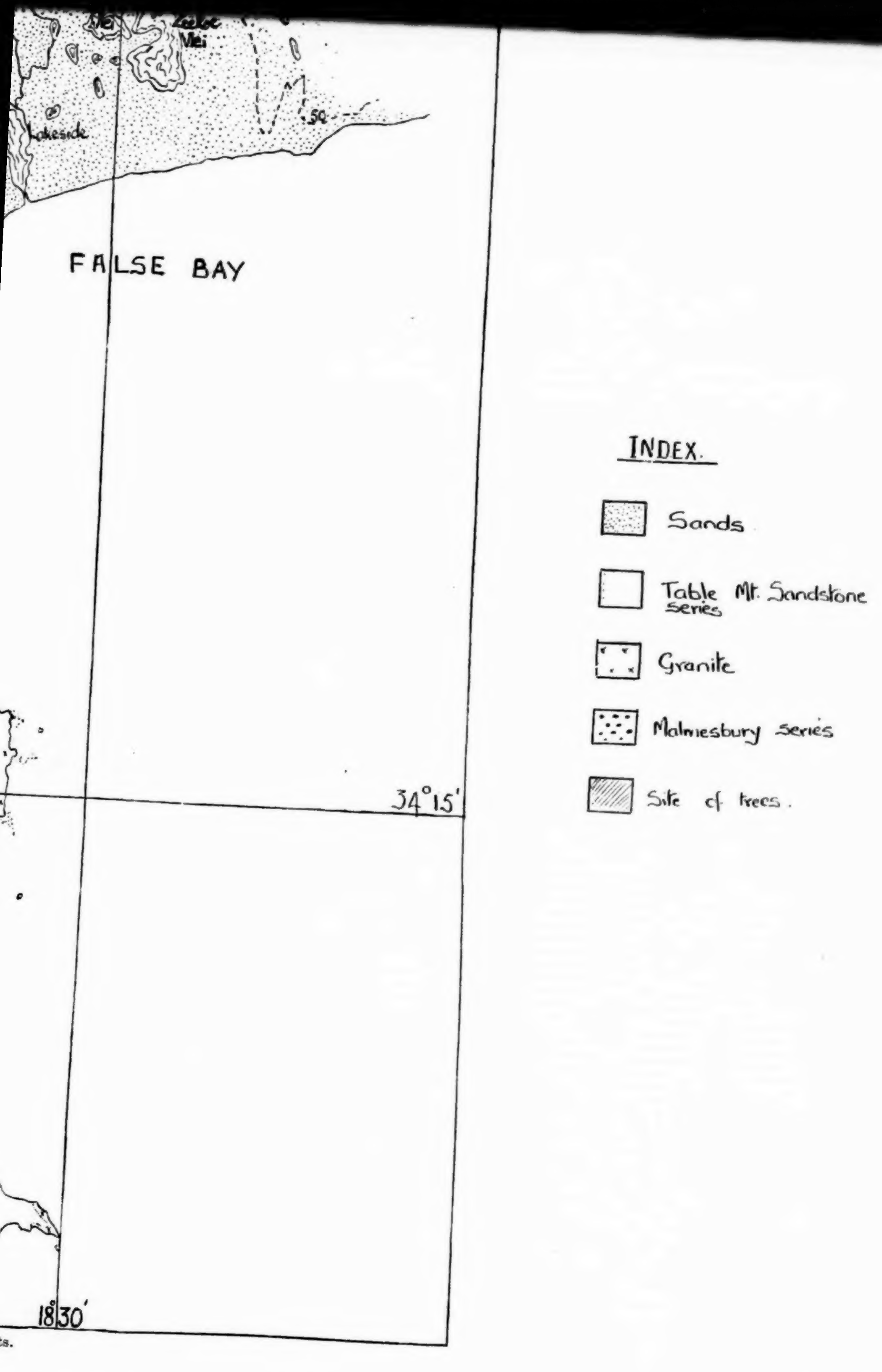


FIG. 1.—The Cape Peninsula and Flats.

R. S. Adamson and M. M. Currin.



Lakeside
Zeekoe Vlei
FALSE BAY
34°15'
18°30'
INDEX.
Sands
Table Mt. Sandstone Series
Granite
Malmesbury series
Site of trees.

[To face p. 13.

BURIED TREES ON THE CAPE FLATS.

By R. S. Adamson and M. M. Currin.

(With Plates VII–X and three Text-figures.)

(Read June 15, 1949.)

The occurrence of tree stems buried in the soil of the Cape Flats is of considerable interest. The discovery was made in the course of excavations for sewers, and our warmest thanks are returned to the Cape Town City Engineer's Department, and especially to Mr. V. L. Granger, the engineer-in-charge, for bringing this occurrence to our notice, and more especially for their having made a complete excavation of the first one found.

In all, four tree trunks were discovered within a distance of 1½ miles in the trench, all in the vicinity of Crawford (fig. 1). Of these four, one was completely exposed and examined, another examined only so far as it was uncovered by the excavation of the trench. The other two, unfortunately, were covered over again before an examination could be made. The first tree was 14 feet below the surface, the second about 11 feet, and the two not examined about 10 and 7 feet respectively. The general land surface where the discovery was made is about 60 feet above sea-level but somewhat irregular. Near the first site was a depression in which water stands in winter. A shallow stream channel occurs about half a mile to the westward.

Tree.

The tree which was fully excavated was a trunk 57 feet long and 4 feet diameter at the base (Pl. VII). It was straight and unbranched, also without roots. The trunk was fluted rather irregularly (Pl. VIII). When removed it was found to be hollowed out below (Pl. IX).

The trunk consisted of wood alone without bark. The structure is remarkably well preserved. The wood is soft and easily cut, and is dark chocolate-brown in colour. When dried it breaks up easily, separating into longitudinal flakes. There is no trace of mineral replacement in the wood.

Microscopic examination shows that the wood is a coniferous timber. There is no clear distinction of annual rings and there are no resin canals.

Scattered parenchyma is associated with the tracheids. While the tracheids show complete structure, the parenchyma cells both in the wood and in the medullary rays have become filled with a brown semi-opaque substance that largely obscures structural details. The rather wide tracheids have uniseriate circular bordered pits with a broadly elliptical central aperture. The pits are not always regularly in line. Paired pits have been seen but are rare. The pits themselves are always separate. Rims of Sanio are present but not at all prominent. The wood parenchyma cells are narrower than the tracheids. The uniseriate medullary rays are numerous; most of them are 3 to 12 cells deep, but there are occasional much deeper rays. When visible the field pits are large and solitary.

In structure and size of the cells this wood agrees wholly with that of *Podocarpus falcatus* R. Br. ex Mirb. (Outeniqua or Common Yellow-wood). It is readily distinguished, both by the size of the tracheids and the form of the medullary rays, from *P. latifolius* R. Br. ex Mirb. (Real Yellow-wood), the only species recorded as indigenous to the Cape Peninsula.

Wood from the second trunk examined was identical in every respect.

Soils.

The first tree from top to base lay at an angle of 18 degrees E. of N. to 18 W. of S. (magnetic). It was also inclined horizontally, the base lying in white clay-sand some 2 feet below the level of the top, which was in a dark brown soil.

The stratification of soils here from ground-level was as follows (fig. 2, *a*):—

(1) 4 feet of white blown sand.
(2) 4 to 5 feet of grey sand, with intercalated humic bands up to an inch in thickness in the first foot.
(3) 2 to 3 feet of compacted black soil, mingled irregularly with a coffee-coloured less compact soil.
(4) 4 feet of white clayey sand—base.

The strata had a somewhat irregular junction, with general slight dip in a N.–S. and stronger dip in a W.–E. direction.

Above the tree, extending nearly to the top of the humic band of dark soil, cross-bedding was well developed (Pl. X). The bedding was irregular, with the strongest direction indicative of water-currents flowing from base to top of tree and minor currents in other directions. The foreset or inclined plane of bedding was in all cases at a low inclination, consonant with conditions of deposition from a rapid current with small load.

From about 18 feet from the base the trunk was completely hollowed

out below, and in place of wood there were dark grey somewhat iridescent nodules mixed with sand. These do not occur at any other point: they are due to replacement by solutions.

Details of Soils.

Samples of soils from around the tree were taken—one of the basal white clay-sand ((4) above) and four of the dark humic band ((3) above). The nodules inside the log were also subjected to tests.

The basal white clay-sand (4) had fairly even granularity, corresponding to a fine sand or silt with considerable admixture of inorganic colloidal clays. The pH varied between 5·5 and 6 and the humus content was low—rough determinations showed variation from 3 to 5 per cent.; the clay near the humic band in the sample tested had a humus content of 4·64 per cent. The fact that the clay-sand became more humic near its junction with the black soil band is probably due to percolation of humic solutions from above, subsequent to the deposition of the humic soils.

Four soil varieties from the humic band (3) were tested: (a) *A grey-black soil* with an even granularity corresponding to a coarse to medium sand. Its pH averaged 4·7 and humus percentage varied from 5·5 to 6 per cent., the exact determination giving a result of 5·83 per cent.

(b) *A brown-black soil*, in which the cross bedding occurred, had extremely variable granularity. Fine sand, coarse sand, and fragments of gravel were all represented. The grains were less even than in any of the other soils, being subangular to angular. This soil was more strongly acid, its pH averaging 3·6. The humic content, however, was comparatively low—the exact determination registering 4·72 per cent. organic matter.

(c) *A coffee-coloured soil*, a fine sand-silt mixture of rather even granularity, had a pH of 4·4 and humus content of 5·28 per cent.

(d) *A compact black soil* of very fine grain had a high proportion of organic colloids. The humus content was 11·28 per cent. The high acidity—pH 3–3·4—was undoubtedly correlated with the large amounts of humic acid present.

The minerals in all the soils were examined. Quartz was the dominant constituent throughout. (No detailed examination was carried out on the clay minerals.) The dense black soil also contained pyrite in small quantities and some magnetite and haematite. The pyrite was probably due to decay by sulphur bacteria, producing sulphur which combined with iron in the water. Excess iron occurred as haematite grains. The magnetite is probably primary.

The four soil varieties in the humic band were not distinctly interbedded.

The lower portion of the humic band, in which the top part of the tree lay, was a grey-black soil. The coffee-coloured and brown soils were quite irregular in outcrop, sometimes intercalated and sometimes vertically juxtaposed. The dense black soil occurred as irregular masses and narrow veins throughout the humic band.

Probable Deposition of the Beds.

The basal clay-sand was deposited under lacustrine conditions. The relatively high alkalinity and low humus content, absence of current bedding and small regular grain size, all indicate still-water conditions.

Little is known of the geological history of the Flats, but it is quite possible that this area was under water (considering its proximity to the 70-foot raised beach), and the water was probably alkaline, due to the recent elevation of the land from the sea.

The fine grain and even granularity of the humic band, and the high proportion of organic matter, are characteristic of deposition from still water and indicate a lacustrine or vlei origin. A shallow-water rather boggy vlei seems most probable.

The band showing cross bedding (current bedding) is clearly alluvial. The angular irregular grains of sand, pebbles, and type of bedding with low inclination of foreset are characteristic of swift streams of small burden.

The overlying grey sand (2) is obviously more recent and probably wind-blown in part. The humic intercalations in the upper foot reflect rapid changes from arid to damp conditions.

The top four feet is of white sand laid down by wind. The present surface is again rather boggy.

It is extremely difficult even to hazard the possible age of these sediments. Almost nothing is known of the Tertiary and Quaternary history of the Flats. Raised beaches at 450, 70, and 20 feet indicate emergence from the sea-bed. The probable course of the stream or river which produced the cross-bedding is not known—it is not, at any rate, in existence to-day. Some system of drainage must, however, have served the Peninsula ranges of mountains at this time.

The preservation of the wood is remarkable. Since the surrounding soils were waterlogged, fungi could not attack the wood and the marked acidity would keep down bacterial decay. The soils were probably even more acid when first laid down—leaching of some of the humic constituents by surface waters has undoubtedly occurred since then.

The dark grey nodules found in the tree where the wood had been destroyed are concretionary, consist largely of quartz and pyrite, and are probably of more recent origin. Iron in solution, precipitated as hydrous

ferrosulphide by bacterial reaction, or as ferrous hydroxide, would with the addition of sulphur from sulphur bacteria produce melinkowite. This is altered to pyrite. Thus waters rich in iron percolating into the humic bed combined with decay sulphides to form the pyritic nodules. This process is thought to have commenced when vlei conditions were at their peak. It also accounts for the pyritic veins in the humic band.

The second tree lay at a depth of about 11 feet. As far as could be determined from the small piece exposed, this tree was of large size and branched. The main bole had a thickness of some 2 feet, the lateral branch being about 1 foot in diameter. The tree lay in a N.-S. direction, cutting across the trench obliquely, with top facing north.

The surrounding soils differed strongly from those round the first tree. They were stratified thus (fig. 2, *b*):

(1) 4 feet blown sand.
(2) 1 to 2 feet compact black soil.
(3) A little coarse sand.
(4) 5 feet clay.
(5) Base—gravels.

Concretionary sulphide nodules (pyritic) were again found near and in the tree.

The samples of clay and gravels ((4) and (5) above) collected showed—

(*a*) Uniformly low humus content except where, marginally around the tree, the rotting wood had produced a grey tinge in the soils.
(*b*) Distinctly acid nature. The gravels averaged pH 3·3 to 3·5, the clay 4 to 5.
(*c*) Indistinct gradation. The gravel at the base of the trench contained no clay. Gradually a larger part of the interstices of the gravel became clay-filled, until this coarse soil graded indistinguishably into clay with gravel bands and finally into pure clay. At a higher level, near the black band, the clay graded into clay-sand.

The minerals in the gravel are quartz with a very little plagioclase felspar.

The clay minerals were not determined.

Deposition.

The gravel was of a typical alluvial kind, rounded to subangular quartz grains predominating. The size of the grain varied from 1 mm. to about 8 cm. in diameter, giving a densely packed sediment, even without the

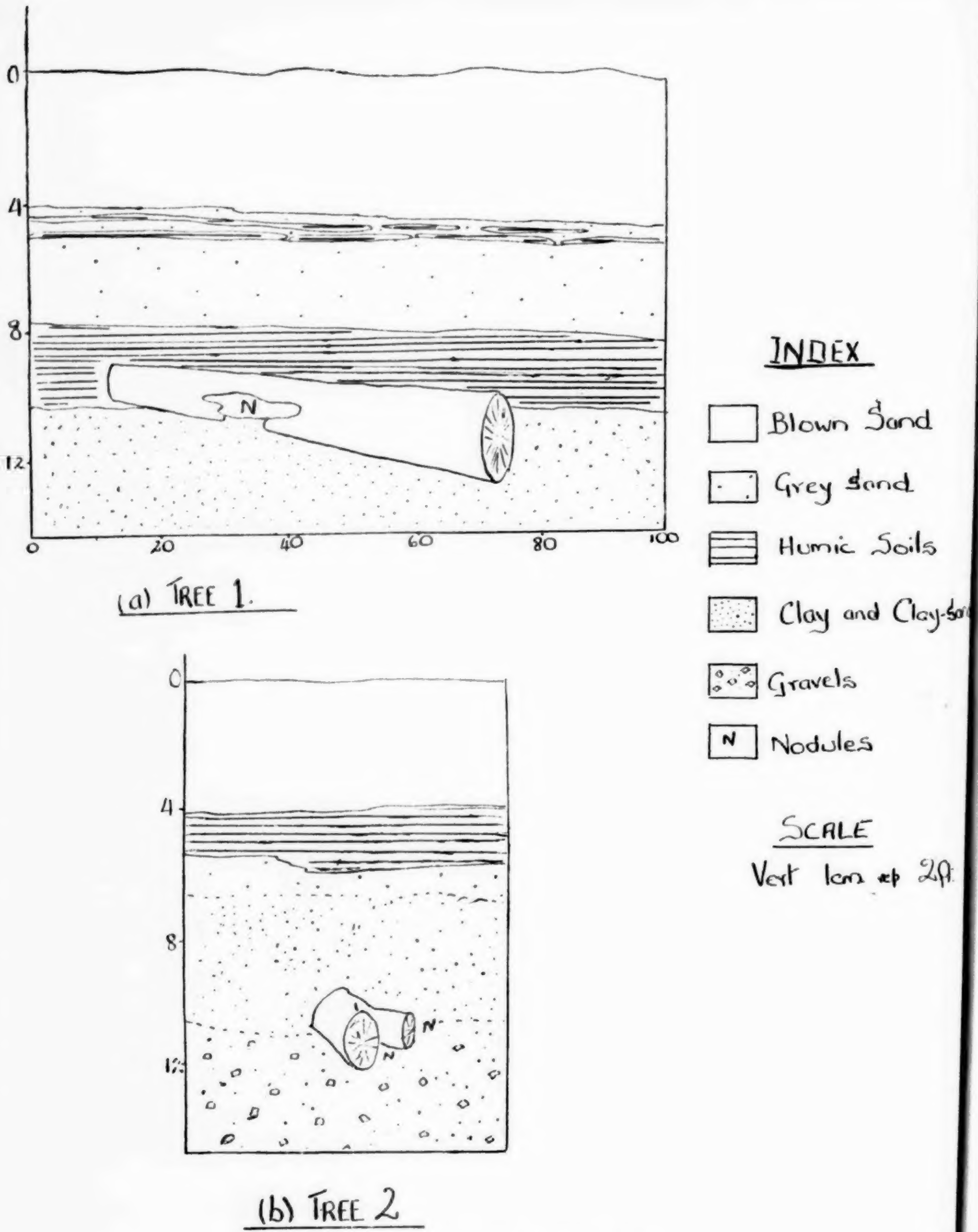


FIG. 2.—Diagrammatic sections of soils.

binding fine sand and clay. The gravel crumbled easily, however, while the clay was very compact, hardening easily to almost a rock when dried.

It is suggested that the gravels were deposited by a young, very swift stream, possibly near its mouth—the absence of current bedding makes all suggestions very liable to contradiction. Later deposition of clay and clay-sand may be alluvial, lacustrine, or marine—the lacustrine conditions being most likely when considering the deposition of the previous tree.

Then a vlei produced the humic soils. A final period of aridity accounted for the blown sand.

Theories on Origin of Trees (see fig. 3).

(1) *Local Origin* (in situ).—Apart from the fact that *Podocarpus falcatus* does not occur west of Swellendam at present and that the habitat is one most unfavourable for large trees, the absence of any traces of roots or stumps makes it most improbable that the trees were growing *in situ*.

(2) *Local Origin* (from mountains).—The present geographical distribution of *P. falcatus* also renders this improbable. It is difficult to imagine the topography of the Peninsula and Flats altering so radically in comparatively recent geological times as to have removed all traces of the existence of a river large enough to carry 60 foot trunks. A similar difficulty exists with regard to the trees having their origin in the Hottentots Holland Mountains.

(3) *Ocean Transport*.—Trees from some point east of Swellendam may have been carried to the sea or to near-sea lagoons, and so out to sea by heavy floods during a season of exceptional south-east storms. Once borne out to sea by flood waters they would be transported by ocean currents to the S.W. Cape. At present, the Agulhas current frequently sweeps right into False Bay during the warmer months of the year, and probably did so in previous times.

The Flats must, at this period, have been at a lower level than at present. The time of emplacement of these trees must have been some time after emergence from the 70-foot beach-level commenced. According to Shand, the sea at this level probably separated the Peninsula from the mainland. Gradual emergence would produce low-lying land, with numerous vleis and lakes covering its surface. The bodies of water were probably interconnected and drained freely. The land may have been higher on the north and lower on the south than it is to-day, so that the drainage was southward rather than northward in the Crawford area. (The Kromboom is a comparatively young river.)

Supporting evidence for the presence of widespread vleis and lakes is

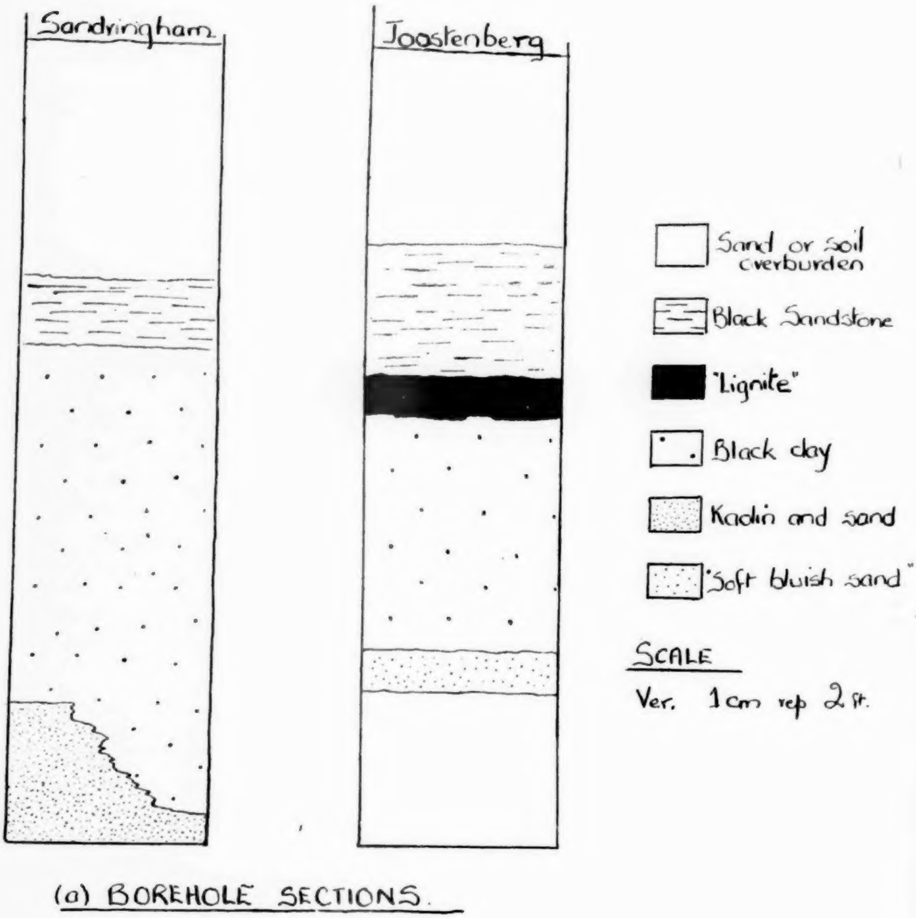

Sandringham
Joostenberg
Sand or soil overburden
Black Sandstone
"Lignite"
Black clay
Kaolin and sand
"Soft bluish sand"
SCALE
Ver. 1cm rep 2 ft.
(a) BOREHOLE SECTIONS.

FIG. 3 (*a*).

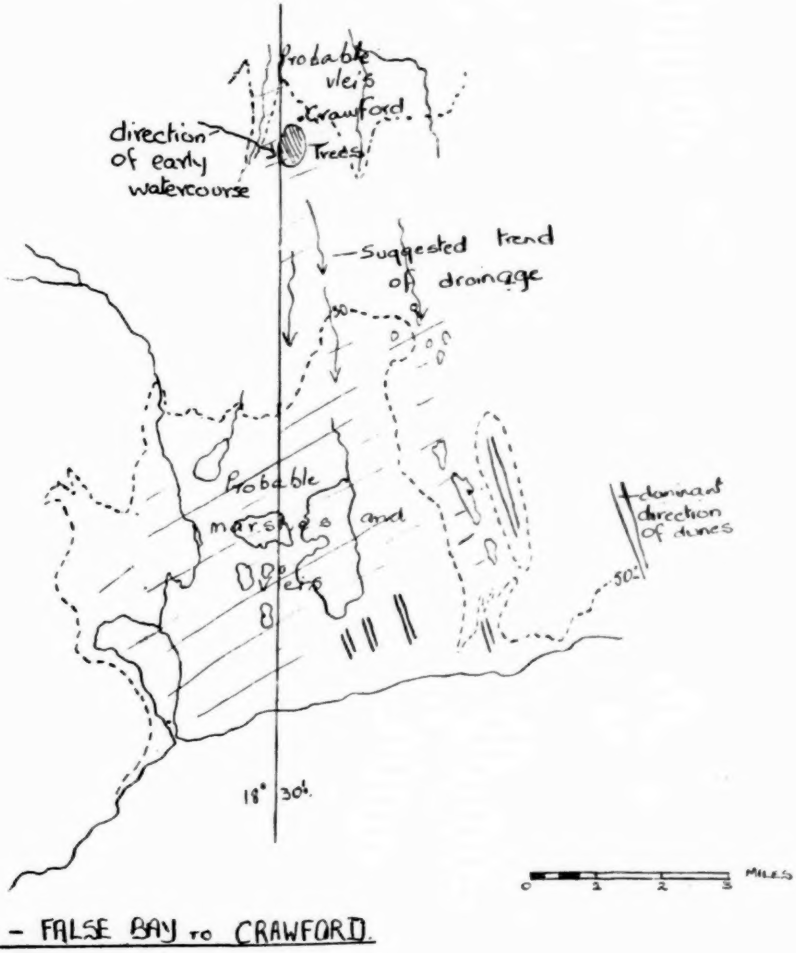

Probable vleis
Crawford
direction of early watercourse
Trees
Suggested trend of drainage
50
Probable marshes and vleis
dominant direction of dunes
50
18° 30'
MILES
0 1 2 3
(b) CAPE FLATS - FALSE BAY TO CRAWFORD.

FIG. 3 (*b*).

revealed by boreholes at Mulders Vlei and Klapmuts (fig. 3, *a*). Strata of black vlei deposits occur there at depths of 7 to 20 feet.

The sewer channel cut across the Flats revealed the frequent occurrence of "coffeestone", a brown soil containing high quantities of organic matter, at varying depths below the surface.

It is presumed, then, that the Flats during this period of high rainfall were drained by a series of interconnected lakes and vleis, which were kept filled partly by seepage and partly by rivers. In other words, the Lakeside, Zeekoe, Ronde, and Princess vleis represent modern relics of the one-time vleis and large lakes on the Flats, cut off from the sea by dunes.

The dunes to-day lie parallel with drainage direction, *i.e.* roughly N.N.W. to S.S.E.: similar dunes in the past would offer very little resistance to the ingress of sea. Exceptional storms from the south-east might break through the dunes and flood the lakes, so carrying the trees inland. (There is a record of a storm in 1847 which caused a major flooding of the Flats by the combined action of flooding streams and rivers, and of waves which beat in from False Bay.) Sudden influx of a large mass of water and the subsequent drainage out to sea would cause very strong currents in the lakes for a considerable time, as they attempted to find a new level or to regain the old. The base of the tree would tend to face downstream in a river bed or vlei, and by virtue of its weight to become anchored first.

Gradual deposition of humic material occurred in the vlei. Flooding by a small river would be sufficient to produce the current bedding.

As to the tree in the river bed, it is thought that the rise of level in the vleis due to the ingress of the sea probably forced the actual river to widen out considerably, and carried the tree upstream some distance and left it near the bank. Filling of the stream bed would be progressive in the river shallows, and the log would soon be covered by gravels.

It is thought that an alteration of levels occurred at this period, the river became very slow, and finally almost still water covered the whole area. The deposition of clays and sands occurred slowly, until several feet of sediment were laid down. A recrudescence of plant life under vlei conditions then gave rise to the upper humic band.

Finally, a local change of drainage and possibly increased aridity caused the vleis to dry up, and blown sand covered the whole area.

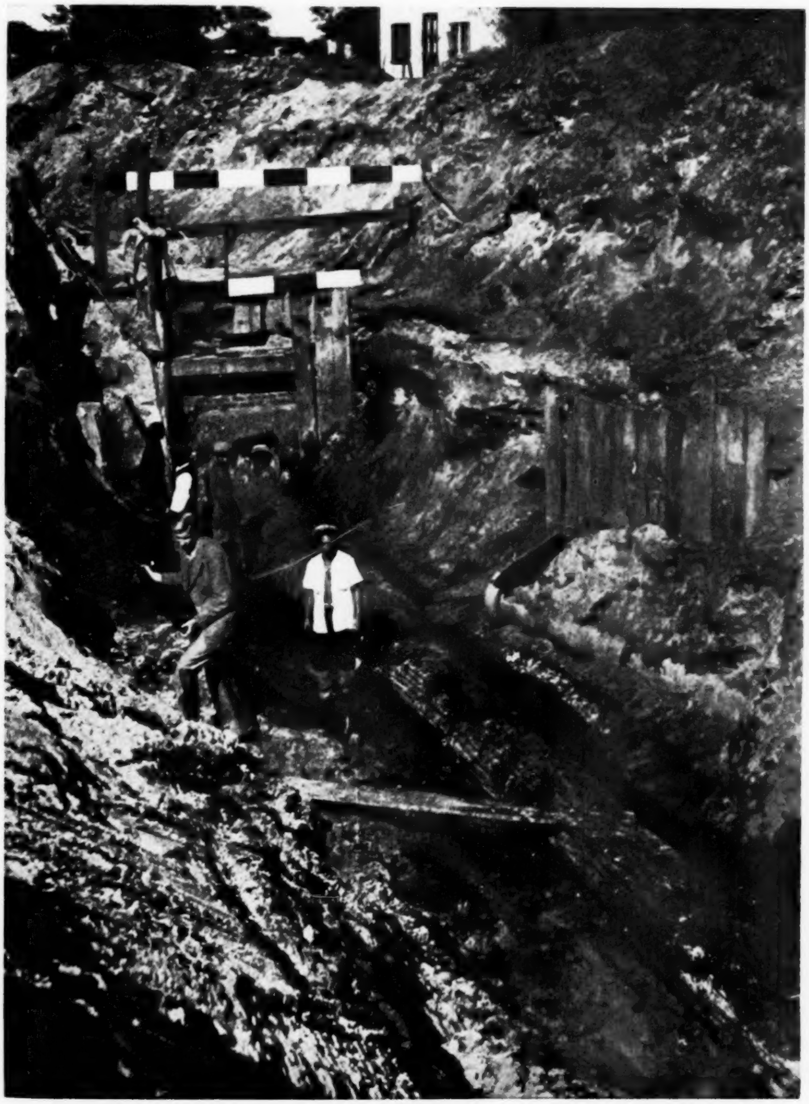
What may be a relic of the watercourse in which the second tree was found is seen about half a mile west. There a modern stream has cut down about 8 to 10 feet and exposed quartzitic gravels and boulders of T.M.S. origin. This is quite consonant with the theory, since the stream on approaching the vlei would reach flatter land and so first drop its boulder and rock burden, then its gravels, and finally discharge its lightened burden of silt and clay into the vlei.

This theory does appear to fit the facts more closely than any other, and is consonant with the views of Shand on the history of the Cape Flats.

Acknowledgments.

We wish to express our grateful thanks to Mr. C. Boocock for the determination of the minerals in the soils and nodules, to Mr. A. O. Fuller for the photographic plates, and to Commander W. J. Copenhagen for the information about the storm in 1847.

The Council desires to acknowledge the receipt of a grant from the University of Cape Town towards the cost of publication of this paper.



The trunk exposed.

Photo: R. S. Adamson and M. M. Currin. *Neill & Co. Ltd.*

Surface of tree.

Photo: R. S. Adamson and M. M. Currin.

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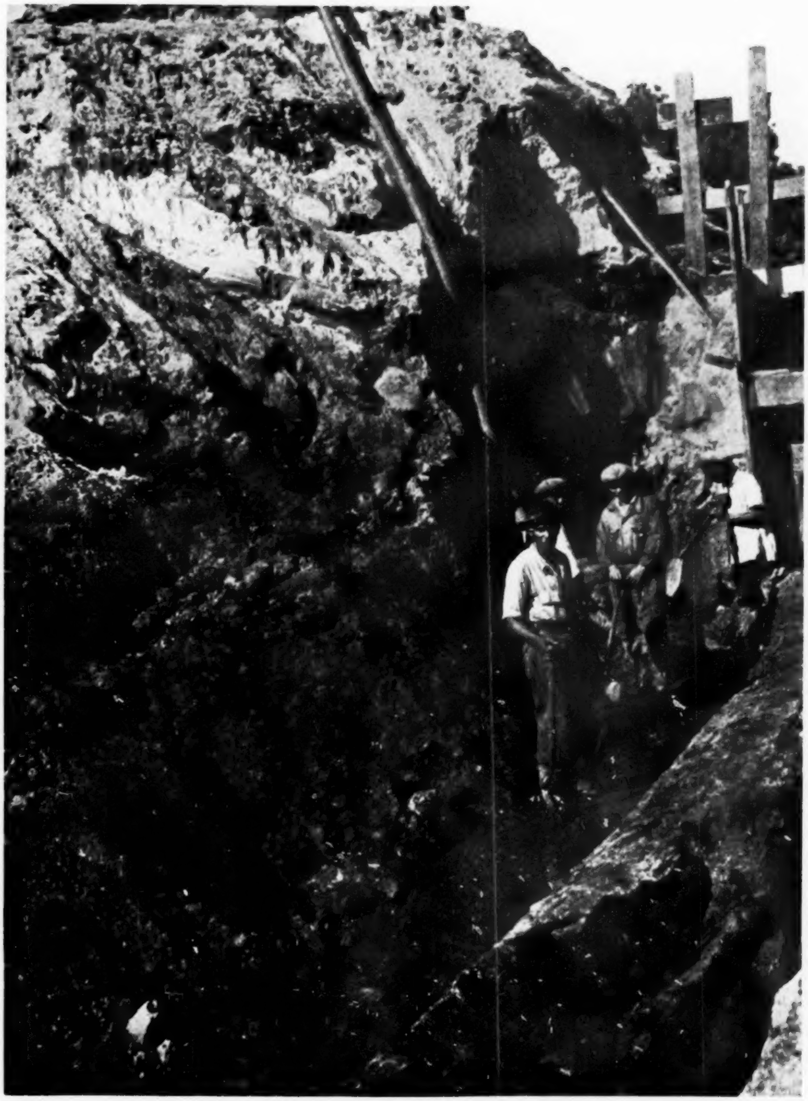

Hollow portion of log where pyritic nodules were found.

Photo: R. S. Adamson and M. M. Currin. *Neill & Co. Ltd.*

Current bedding in upper part of humic band.

Photo R. S. Adamson and M. M. Currin.

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CAPE CHEMICAL SOCIETY

MARLOTH MEMORIAL

GASEOUS EQUILIBRIA AT CONSTANT PRESSURE.

By EDGAR NEWBERY, Department of Physical Chemistry, University of Cape Town.

(Read October 19, 1949.)

The study of gaseous equilibria has generally been carried out under conditions of constant volume, and little attention has been paid to similar systems under conditions of constant pressure.

In view of the fact that many important manufacturing processes (*e.g.* sulphuric acid, ammonia synthesis and oxidation, the blast furnace, etc.) are carried out under conditions much more nearly approaching constant pressure than constant volume, this neglect appears unfortunate, although it is recognised that experimental checking in the laboratory of theoretical conclusions is subject to special difficulties in this case.

It is generally assumed that the addition of excess of one of the products of dissociation invariably lowers the degree of dissociation. This is certainly true for additions at constant volume, but when the addition is made at constant pressure, the increase in total volume tends to increase the dissociation, and in some cases it is possible that this effect may predominate.

Lewis, in his textbook *A System of Physical Chemistry* (1918 ed.), vol. i, p. 152, attempted to solve this problem, but based his work on the incorrect assumption that the total pressure of a gas mixture is unaltered when one component is added at the same partial pressure as that in the mixture. In a later impression of the same edition (1929) the treatment is modified, but the original problem is left unsolved. Other more modern textbooks do not even mention this problem.

The case which presents most difficulty is that in which one substance

dissociates into three, two of which are identical. Ammonium carbamate is a good example, and this has been studied experimentally by Isambert (Compt. Rend., **97,** p. 1212, 1883) and by Briggs (J. Phys. Chem., **28,** p. 1121, 1924), but only under conditions of constant volume.

Consider 1 gm.-mol. (v litres) of ammonium carbamate vapour dissociating at constant temperature and pressure.

Note that v in this work denotes the volume of 1 mol. of a *single* gas at the fixed temperature and pressure of the experiment. It is *not* the total volume of the system.

If the degree of dissociation be denoted by x, we have

	NH_2COONH_4	$\rightleftharpoons$ $2NH_3$	+ CO_2	
Mols. . . .	$1-x$	$2x$	x	
Litres . . .	$(1-x)v$	$2xv$	xv	Total $(1+2x)v$
Concentrations .	$\dfrac{(1-x)}{(1+2x)v}$	$\dfrac{2x}{(1+2x)v}$	$\dfrac{x}{(1+2x)v}$	

Assuming that activities are proportional to concentrations, the equilibrium constant is given by

$$K=\frac{4x^3}{(1-x)(1+2x)^2v^2}.$$

Now add n mols. (nv litres) of CO_2 at the same pressure. The total volume is momentarily increased to $(1+2x+n)v$ litres, and momentary concentrations now become

$$\frac{(1-x)}{(1+2x+n)v} \qquad \frac{2x}{(1+2x+n)v} \qquad \frac{(x+n)}{(1+2x+n)v}.$$

The momentary state is now represented by

$$K'=\frac{4x^2(x+n)}{(1-x)(1+2x+n)^2v^2}=\frac{4x^3\left(1+\dfrac{n}{x}\right)}{(1-x)(1+2x)^2v^2\left(1+\dfrac{n}{1+2x}\right)^2}$$

$$=K\frac{1+\dfrac{n}{x}}{\left(1+\dfrac{n}{1+2x}\right)^2}.$$

Now the difference between the top and bottom of this fraction will be zero if no change of dissociation occurs, $+ve$ if dissociation is reduced,

and $-ve$ if dissociation is increased by the specified addition. This difference is given by

$$D = 1 + \frac{n}{x} - 1 - \frac{2n}{1+2x} - \frac{n^2}{(1+2x)^2}$$
$$= \frac{n(1+2x-nx)}{x(1+2x)^2}.$$

This expression becomes zero when $n = 1/x + 2$, and under these conditions the diluting effect of the added gas lowering the partial pressure of the NH_3 exactly balances the concentrating effect on the CO_2. If more CO_2 is now added, dissociation will be increased.

Since D is also zero when $n = 0$, the dissociation will attain a minimum when $n = 1/2x + 1$, and D then has the value $1/4x^2$.

This may be proved by putting $n = a + 1 + 1/2x$ in the above equation for D, when it is found that $D' = 1/4x^2 - a^2/(1+2x)^2$, which must be less than D for all values of a.

The addition of excess NH_3 has a markedly different effect. If n mols. of NH_3 are added under the same conditions, a similar calculation shows that the momentary state is now represented by

$$K' = K \cdot \frac{1 + \frac{n}{x} + \frac{n^2}{4x^2}}{\left(1 + \frac{n}{1+2x}\right)^2}.$$

The difference between the top and bottom of this fraction is

$$D = \frac{(n + 4x + 4nx + 8x^2)n}{4x^2(1+2x)^2}.$$

Since n and x are always $+ve$ quantities, K' is always greater than K. Hence the addition of excess NH_3 at constant pressure always depresses the dissociation.

In the case of a single substance dissociating into three *different* products, similar calculation shows that the addition of any one of the products of dissociation has the same effect as the addition of CO_2 in the carbamate system, dissociation being at a minimum when $n = 1/2x + 1$.

For a first type gas reaction

$$2A \rightleftharpoons B + C,$$

it may be shown in the same way that

$$K' = K + \frac{nx}{4(1-x)^2}.$$

Lastly, in the simple second type gas reaction,

$$A \rightleftharpoons B + C,$$

$$K' = K \times \frac{1 + \frac{n}{x}}{1 + \frac{n}{1+x}}.$$

Hence in both these cases dissociation is always diminished by the addition of excess of either B or C at constant pressure.

Summary.

When one molecule of a gas dissociates into three different parts, if n gm.-mols. of one of the products of dissociation is added to 1 gm.-mol. of the original gas at constant temperature and pressure, the degree of dissociation attains a minimum when $n = 1/2x + 1$, where x represents the original degree of dissociation.

If n exceeds $1/x + 2$, the dissociation is increased by the addition.

When one molecule of a gas dissociates into three parts, two of which are identical, addition of the dissimilar product under the same conditions follows the same law, but addition of the other product always depresses the dissociation.

In bi-molecular dissociations, whether first or second type, addition of either product at constant temperature and pressure always depresses the dissociation.

Acknowledgment.

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CRANIOMETRIC STUDY OF THE CAPE COLOURED POPULATION.

By J. A. Keen,
Department of Anatomy, University of Cape Town.

(With Plate XI and three Text-figures.)

(Read November 16, 1949.)

The Cape Coloured people inhabit Cape Town, the Cape Peninsula and the western corner of the Cape Province. Their emergence as a distinct ethnic group is a matter of history, covering a time-period of three centuries. The basis of the Cape Coloured group is the original Hottentot population, and an early admixture occurred between the incoming European settlers and the Hottentots. The Hottentot people at that time were already a somewhat mixed racial group, having absorbed a good deal of Bushman blood (Maingard, 1932). The Bushman element in the genetic make-up of the Cape Coloured will be seen to be an important factor.

A further admixture occurred when the Dutch East India Company introduced slaves into the colony. Some of the slaves came from population groups in the far East, such as Java, or the nearer East, such as Ceylon and India, and they brought into the Cape Coloured group elements of the south-eastern races of Asia. Other slaves came from the east coast of Africa along the trade route of the Dutch East India Company, and these brought a negro element into the racial make-up of the Cape Coloured. It should be noted, however, that this is not the same as the West African negro element which has entered into the formation of the mixed racial groups of the American continent. The East African negro populations contain a considerable admixture of Hamitic stock which differentiates them from the West African negro communities.

In the main, therefore, the Cape Coloured people contain a mixture of Hottentot, Bushman, European, Asiatic and Negro racial elements, the crossings between these major subdivisions of mankind being well established and having occurred within a comparatively short time-period. To such

population groups the term "hybrid" should be applied (Trevor, 1938), in order to distinguish them from other less mixed or relatively "pure" racial groups. It will be shown in this craniometric study that the Cape Coloured people, in spite of their very mixed origin, are a stabilized human group and that they have become as homogeneous physically as the other racial groups which have contributed to their evolution.

Material.—This study is based on the measurements of crania obtained from dissecting-room cadavers, and was undertaken by permission of Professor M. R. Drennan. About 65 per cent. of the subjects which reach the Anatomy Department are individuals classed as Cape Coloured, and of the 201 adult crania which were measured, 141 came from males and 60 from females. The sex of each skull was therefore known, a fact which it is necessary to emphasize in an anthropological study of crania.

Standard Set of Measurements.—Before beginning this investigation a standard set of measurements had been chosen, consisting of the more usual cranium and face dimensions which are employed in physical anthropology. The first twelve sections in Tables I and II are dimensions and indices which concern the *vault* of the skull. The length of the mastoid process (No. 11) is obtained by drawing a line across the root of the mastoid process parallel to the Frankfort plane, at the level of the upper margin of the suprameatal triangle, and then measuring the vertical distance between a point on that line and the tip of the mastoid process. If the suprameatal triangle is ill-defined, the level of the upper margin of the external auditory meatus is used.

There are eleven measurements and six indices (Nos. 13–29) which concern the *facial part* of the skull and are designed to study the configuration of the orbit, nose and mandible. All these are well-recognized measurements, except the minimum ramus breadth and minimum ramus height of the mandible. The minimum ramus breadth is the smallest distance obtainable between the front edge and the posterior border of the ramus. The minimum ramus height is the distance between the lowest point of the mandibular notch and the lower border of the mandible, the measurement being made along a line at right angles to the line of the minimum ramus breadth measurement. These two mandible dimensions and an index obtained from them have been shown to have a special significance in the differentiation between Hottentot, Bushman and Bantu crania (Keen, 1947). The angle at the nasion (No. 29) is the forward angle formed at the nasion between straight lines joining nasion to glabella and nasion to rhinion; a simple method of measuring this angle has been described (Keen, 1949).

TABLE I.—SHOWING THE RANGE, MEAN AND STANDARD DEVIATION OF THE CRANIAL AND FACIAL MEASUREMENTS IN A GROUP OF 141 MALE AND 60 FEMALE SKULLS OF THE CAPE COLOURED POPULATION.

	Male (141 Skulls).	Female (60 Skulls).
1. Maximum length:		
Range	159–205 mm.	161–193 mm.
Mean	184·0 ± ·6 mm.	177·6 ± ·8 mm.
Standard deviation	7·0 mm.	6·5 mm.
2. Maximum breadth:		
Range	122–151 mm.	121–146 mm.
Mean	135·5 ± ·4 mm.	132·7 ± ·8 mm.
Standard deviation	5·1 mm.	5·9 mm.
3. Minimum frontal breadth:		
Range	84–105 mm.	81–102 mm.
Mean	95·7 ± ·4 mm.	93·4 ± ·6 mm.
Standard deviation	4·6 mm.	4·4 mm.
4. Basion-bregma height:		
Range	118–145 mm.	117–139 mm.
Mean	131·3 ± ·4 mm.	127·0 ± ·6 mm.
Standard deviation	5·3 mm.	4·9 mm.
5. Breadth/length index (2 : 1):		
Range	60·0–80·8	68·8–80·2
Mean	73·6 ± ·3	74·8 ± ·4
Standard deviation	3·3	3·0
6. Height/length index (4 : 1):		
Range	62·5–78·6	67·0–76·4
Mean	71·5 ± ·3	71·4 ± ·3
Standard deviation	3·3	2·6
7. Height/breadth index (4 : 2):		
Range	84·9–117·8	87·0–104·9
Mean	97·1 ± ·4	95·9 ± ·5
Standard deviation	4·8	4·0
8. Transverse fronto-parietal index (3 : 2):		
Range	61·3–81·3	63·9–79·4
Mean	70·6 ± ·3	70·4 ± ·5
Standard deviation	3·6	3·6

TABLE I—*continued.*

	Male (141 Skulls).	Female (60 Skulls).
9. Horizontal circumference:		
Range	463–548 mm.	454–530 mm.
Mean	513·1 ± 1·2 mm.	496·6 ± 2·0 mm.
Standard deviation	14·8 mm.	15·8 mm.
10. Cranial capacity:		
Range	1010–1750 c.c.	860–1545 c.c.
Mean	1335·6 ± 10·6 c.c.	1193·6 ± 16·9 c.c.
Standard deviation	124·1 c.c.	129·8 c.c.
11. Length of mastoid process:		
Range	20–37 mm.	18–33 mm.
Mean	28·8 ± ·3 mm.	26·5 ± ·4 mm.
Standard deviation	3·3 mm.	3·4 mm.
12. Length of base:		
Range	87–116 mm.	82–101 mm.
Mean	100·3 ± ·4 mm.	94·8 ± ·5 mm.
Standard deviation	4·5 mm.	4·2 mm.
13. Length of face:		
Range	83–118 mm.	77–105 mm.
Mean	98·3 ± ·6 mm.	94·4 ± ·8 mm.
Standard deviation	6·6 mm.	5·9 mm.
14. Gnathic index (13 : 12):		
Range	86·5–107·2	88·5–110·6
Mean	98·1 ± ·4	99·6 ± ·6
Standard deviation	4·7	4·7
15. Maximum bizygomatic diameter:		
Range	116–141 mm.	105–130 mm.
Mean	128·1 ± ·4 mm.	119·3 ± ·7 mm.
Standard deviation	5·2 mm.	5·4 mm.
16. Total height of face:		
Range	100–139 mm.	90–127 mm.
Mean	115·8 ± ·7 mm.	108·5 ± 1·2 mm.
Standard deviation	8·4 mm.	8·9 mm.
17. Upper face height:		
Range	57–83 mm.	53–74 mm.
Mean	67·9 ± ·4 mm.	65·1 ± ·7 mm.
Standard deviation	5·0 mm.	5·0 mm.

TABLE I—*continued.*

	Male (141 Skulls).	Female (60 Skulls).
18. Total facial index (16 : 15):		
Range	78·4–105·6	75·5–105·9
Mean	90·5 ± ·5	90·7 ± ·9
Standard deviation	6·5	6·4
19. Upper facial index (17 : 15):		
Range	43·3–62·0	45·4–62·2
Mean	52·9 ± ·3	54·2 ± ·5
Standard deviation	3·8	3·5
20. Breadth of orbit:		
Range	39–47 mm.	36–45 mm.
Mean	43·0 ± ·2 mm.	41·4 ± ·2 mm.
Standard deviation	1·8 mm.	1·9 mm.
21. Height of orbit:		
Range	27–39 mm.	27–36 mm.
Mean	32·9 ± ·2 mm.	32·7 ± ·3 mm.
Standard deviation	2·3 mm.	2·0 mm.
22. Orbital index (21 : 20):		
Range	65·1–89·[illegible]	67·5–89·7
Mean	76·6 ± ·4	79·0 ± ·5
Standard deviation	4·8	4·0
23. Nasal width:		
Range	20–33 mm.	21–[illegible] mm.
Mean	26·3 ± ·2 mm.	25·0 ± [illegible] mm.
Standard deviation	2·3 mm.	2·2 mm.
24. Nasal height:		
Range	34–57 mm.	36–52 mm.
Mean	49·2 ± ·3 mm.	46·6 ± ·4 mm.
Standard deviation	3·3 mm.	3·4 mm.
25. Nasal index (23 : 24):		
Range	35·1–67·6	44·7–68·4
Mean	54·2 ± ·5	54·6 ± ·7
Standard deviation	5·5	5·5
26. Minimum ramus breadth:		
Range	22–44 mm.	17–37 mm.
Mean	32·9 ± ·3 mm.	30·0 ± ·5 mm.
Standard deviation	4·1 mm.	3·7 mm.

TABLE I—*continued.*

	Male (141 Skulls).	Female (60 Skulls).
27. Minimum ramus height:		
Range	36–61 mm.	30–57 mm.
Mean	47·1 ± ·4 mm.	42·8 ± ·7 mm.
Standard deviation	4·5 mm.	5·8 mm.
28. Index of ramus (26 : 27):		
Range	47·5–100·0	48·3–103·3
Mean	70·2 ± ·9	70·9 ± 1·5
Standard deviation	10·9	11·9
29. Angle at nasion:		
Range	98°–162°	124°–162°
Mean	136·3° ± 1·1°	145·8° ± 1·24°
Standard deviation	12·5°	8·8°

DATA OF OTHER RACIAL GROUPS USED FOR COMPARISON.

In order to be able to investigate the racial affinities of the Cape Coloured people in various directions, I had first of all obtained the measurements of the following groups of crania.

(1) The dimensions of the *Hottentot* and *Bushman* crania were obtained from collections of Hottentot and Bushman skulls in the National Museum, Bloemfontein, and in the Anatomy Department of the University of Cape Town; there was no sex differentiation among these.

(2) A *Bantu* group of skulls were measured in the Anatomy Department of the University of the Witwatersrand, by kind permission of Professor R. A. Dart. The crania belong to a collection of skeletons from dissecting-room subjects, and altogether 220 adult male skulls of known sex were measured. The data thus represent a sample of the present-day male Bantu population of Johannesburg. In the present craniometric study I have used these Bantu data to represent the Negro element in the racial inheritance of the Cape Coloured people. By this it is not implied that the Bantu, that is the South African Negros, are an important element in the evolution of the Cape Coloured population. As explained above, the Negro racial element was introduced through the African slaves brought to the Cape from the east coast.

(3) A group of *European* skulls from a collection at the Musée de l'Homme, Paris, which were measured by kind permission of Professor P. Lester, the Director of the Anthropological Section of the Musée de l'Homme.

Table II.—Showing the Means of the Cranial and Facial Measurements and Indices in the Four Groups of Skulls used for Comparison.

	Bantu (220 Skulls).	European (186 Skulls).	Hottentot (35 Skulls).	Bushman (31 Skulls).
1. Maximum length	187·0 mm.	184·0 mm.	192·0 mm.	174·7 mm.
2. Maximum breadth	133·6 mm.	143·6 mm.	135·0 mm.	132·6 mm.
3. Minimum frontal breadth	97·3 mm.	98·4 mm.	98·1 mm.	91·9 mm.
4. Basion-bregma height	133·8 mm.	132·4 mm.	132·3 mm.	121·8 mm.
5. Breadth/length index (2 : 1)	71·6	78·1	70·5	75·8
6. Height/length index (4 : 1)	71·6	72·1	69·0	69·8
7. Height/breadth index (4 : 2)	100·1	92·4	97·3	92·0
8. Transverse fronto-parietal index (3 : 2)	72·8	68·5	72·8	69·3
9. Horizontal circumference	517·0 mm.	521·4 mm.	524·6 mm.	489·0 mm.
10. Cranial capacity	1374·0 c.c.	1459·1 c.c.	1434·3 c.c.	1163·1 c.c.
11. Length of mastoid process	28·6 mm.	31·0 mm.	25·2 mm.	22·5 mm.
12. Length of base	101·7 mm.	100·5 mm.	102·9 mm.	92·4 mm.
13. Length of face	102·8 mm.	96·7 mm.	101·8 mm.	91·4 mm.
14. Gnathic index (13 : 12)	101·4	96·4	98·9	99·2
15. Maximum bizygomatic diameter	129·8 mm.	131·0 mm.	128·7 mm.	119·4 mm.

TABLE II—*continued.*

	Bantu (220 Skulls).	European (186 Skulls).	Hottentot (35 Skulls).	Bushman (31 Skulls).
16. Total height of face	117·1 mm.	117·0 mm.	113·8 mm.	97·9 mm.
17. Upper face height	69·1 mm.	70·7 mm.	67·0 mm.	58·6 mm.
18. Total facial index (16 : 15)	90·5	89·5	89·1	82·3
19. Upper facial index (17 : 15)	53·4	53·9	52·4	49·3
20. Breadth of orbit	43·3 mm.	41·7 mm.	43·5 mm.	41·0 mm.
21. Height of orbit	33·3 mm.	32·8 mm.	32·6 mm.	30·8 mm.
22. Orbital index (21 : 20)	77·1	78·9	74·9	75·2
23. Nasal width	28·0 mm.	23·6 mm.	27·8 mm.	25·8 mm.
24. Nasal height	49·4 mm.	51·0 mm.	47·7 mm.	42·2 mm.
25. Nasal index (23 : 24)	57·0	47·1	58·4	61·3
26. Minimum ramus breadth	35·5 mm.	31·5 mm.	40·6 mm.	33·8 mm.
27. Minimum ramus height	48·0 mm.	51·8 mm.	45·1 mm.	39·9 mm.
28. Index of ramus (26 : 27)	74·3	61·2	88·9	85·0
29. Angle at nasion	138·0°	125·6°	155·9°	154·4°

These crania mostly came from graves in Paris or from the immediate neighbourhood, and are representative of the French population living in or near Paris in modern times. In this European group (186 skulls) the sex was not known and no sexual differentiation on visible skull characteristics was attempted. Such a proceeding is recognized to be unreliable, unless differential sexual data for the particular racial group are available.

The same standard set of measurements had been applied to these other

groups of crania. The means of the various dimensions for the four different racial groups are seen in Table II. Owing to the influence of personal equation it is of advantage if the measurements have all been made by the same observer; this applies in the present instance.

Data obtained by other Observers.

Cape Coloured Group.—A group of living Cape Coloured, all male, was studied anthropometrically by van Wyk (1939), and these individuals came from Stellenbosch, which is thirty-one miles distant from Cape Town. It seemed of some importance to ascertain whether the data obtained by this author and the present skull data from a dissecting-room group could be looked upon as samples taken from the same population group. The mean standing height, which all anthropologists consider as an extremely important characteristic for separating different ethnic groups, was used as a criterion. The measurement of standing height could not be obtained directly in my material, but the cadaver length was measured as a routine when the subjects reached the Anatomy Department. In order to convert cadaver length into standing height, 2 cm. was deducted in each case, an adjustment recommended in Martin's text-book (1928). The mean standing height of 95 male Cape Coloureds from the dissecting-room group, obtained in this manner, was 162 cm. The mean standing height of the Stellenbosch group of living Cape Coloured (133 males), measured by van Wyk, was 162·2 cm.; thus there was an extremely close approximation between the two groups.

From the point of view of stature the various populations of the world are divided into three main groups—tall, medium and small—and each of these is further split up into three subdivisions (Martin, 1928). A mean standing height of 162 cm. (5 ft. 4½ in.) for the males, places the Cape Coloured population into the lowest subdivision of medium height peoples ("*untermittelgross*").

van Wyk (1939) suggested that the Cape Coloureds in the immediate vicinity of Cape Town might contain a higher proportion of the so-called "Ind.-Hott." types, that is Cape Coloured persons with a specially large admixture of Asiatic stock, and might therefore differ somewhat from a Cape Coloured group living more inland, as at Stellenbosch. Judging from the very close means for the standing height this is probably not the case. Neither van Wyk's group of living Cape Coloured males nor the present dissecting-room group contained any Cape Malays. The Cape Malays live mostly in Cape Town and its suburbs, and they have crystallized out from the Cape Coloureds as a separate entity on religious grounds. For the same reason they never reach the dissecting room, because the Muslim religion forbids the mutilation of the body after death.

When making comparisons between head dimensions and corresponding skull dimensions, it is necessary to make an allowance for the soft-part coverings, as follows: for maximum length a difference of 7 mm., for maximum breadth and maximum bizygomatic diameter a difference of 6 mm., for horizontal circumference (if near 500 mm.) a difference of 30 mm. (Martin, 1928).

If the means obtained for some of the head dimensions of the living Cape Coloured males are placed side by side with those of the corresponding skull measurements, and with the corrections for the soft parts (Table III), a very

TABLE III.—SHOWING THE MEANS OF CERTAIN HEAD MEASUREMENTS OF CAPE COLOURED MALES, COMPARED WITH THE MEANS OF THE CORRESPONDING SKULL MEASUREMENTS OF THE MALES OF THE SAME POPULATION GROUP.

	Means from van Wyk's Group of Cape Coloured (133 Males).	Means from Cape Coloured Skull Measurements (141 Male Skulls).	Usual Allowance made for Soft Parts.
Maximum length	191 mm.	184 mm.	7 mm.
Maximum breadth	147 mm.	136 mm.	6 mm.
Minimum frontal breadth	101 mm.	96 mm.	6 mm.
Maximum bizygomatic diameter	133 mm.	128 mm.	6 mm.
Horizontal circumference	560 mm.	513 mm.	30 mm.

close similarity is seen in the figures for maximum length, minimum frontal breadth, maximum bizygomatic diameter, and a fairly close one for horizontal circumference. But an unexpected discrepancy appeared in the maximum breadth measurements which is difficult to explain. It is well known that the dimension of maximum breadth is subject to a greater personal error than the other measurements, because no fixed points on the head or skull are used; a very little obliquity in the placing of the caliper points can result in differences in reading up to 3 mm. Further, the points where the measurements are taken come within the area of the temporal muscle attachment, and the soft-part coverings here must be thicker than, *e.g.*, the skin over the glabella or over the zygomatic arches; the allowance

for the soft parts in the maximum breadth dimension should perhaps be 8–10 mm., instead of 6 mm. (4–5 mm. on each side). Such a correction would make the maximum breadth means fairly similar in the two groups of male Cape Coloured.

European Group.—The means obtained for the various dimensions and indices of the group of crania measured in Paris may be compared with the figures given for other European groups. For instance, the means for *maximum length* for various European population groups (not French) are given as 178, 180, 187, 193 (average 184·5 mm.) in males, and as 172, 179, 173, 184 (average 177·0 mm.) in females (Martin, 1928). For *maximum breadth* the figures 148, 149, 150 (average 149·0 mm.) are given in males, and 143, 138, 145 (average 142·0 mm.) in females. For *basion-bregma height* 133, 133, 132 (average 132·7 mm.) in males, and 128, 126, 126 (average 126·7 mm.) in females. The corresponding figures in the second column of Table II show that the means which were obtained lie between the male and female means given above. From this it may be deduced that the group of European skulls which was measured contained both male and female crania. The mean *horizontal circumference* in adult European skulls (male) is given as 520 mm. (Martin, 1928). The above data quoted from the available literature show that the means obtained from the Paris group of crania can be considered as representative of European skull dimensions.

Hottentot and Bushman Groups.—Anthropologists are not in agreement as to the precise definition and delimination of these two racial groups. One school of anthropologists takes the view that the Hottentots and Bushmen are so much alike in physical characters that one must look upon them as closely allied subgroups of the so-called *Khoisan race* (Schapera, 1930; Galloway, 1933). The opposing school of anthropologists (Broom, 1923; Dreyer, 1937; Drennan, 1938) considers that the Hottentots and Bushmen are sharply differentiated racial groups, and that confusion has arisen through extensive hybridization of the two peoples. Further confusion has arisen through the use of the terms *Korana* and *Strandloper* in a racial sense; both these terms should be considered as synonymous with Hottentot (Keen, 1942, 1943). Thus it will be clear that previous data bearing on Hottentot and Bushman crania are not always helpful.

In this study the Hottentots and Bushmen have been treated as two strongly differentiated population groups, and the view is taken that their hereditary influence on the skull characteristics of the Cape Coloured must be considered separately. The pure Hottentot type shows a large skull, narrow in the forehead region and markedly dolichocephalic, with a long face and a massive mandible; while the typical Bushman has a small cranium with a straight forehead outline, a tendency to brachycephaly, a short face and a delicate mandible.

Cape Coloured Skull Dimensions related to those of other Racial Groups.

In figs. 1 and 2 the means of the various dimensions and indices have been arranged in such a way that the relative position of the Cape Coloured male and female groups of crania is easily seen; of the 29 dimensions and indices, 19 are represented in these figures. The differences between the various means are not great, but in each instance the difference between the maximal and minimal values is represented by the vertical distance between the two horizontal lines.

Plate XI is a photograph of one of the male Cape Coloured skulls seen in front view and left lateral side view. The skull was chosen as representative because a specially large number of its dimensions and indices were near the means for the group.

Sexual Differences.—The sexual differences found in the Cape Coloured crania are very similar to those found on analysis of other series of crania. For instance, in most racial groups the female skull on the average has a slightly higher *breadth/length index*, and is thus inclined towards brachycephaly as compared with the male (Martin, 1928); the Cape Coloured skulls follow the general rule (fig. 1). The difference in *cranial capacity* between the sexes is said to average 150 c.c., in some races up to 200 c.c.; in the Cape Coloured the mean difference was 140 c.c.

The *gnathic index* is a little higher in the female than in the male (fig. 2), due mainly to the smaller length of base, which is the denominator in this index. The sexual difference for the length of the base is relatively greater than for the length of the face (Table I). The *total facial index* is the same for the two sexes, the face being relatively long in the Cape Coloureds (Plate XI). The *angle at the nasion* is somewhat wider in the female than in the male; this is correlated with the fact that the prominent glabella is a male secondary sexual character, evident in all racial groups.

Racial Differences (figs. 1 and 2).—As regards *maximum length* the male Cape Coloured stands about half-way between the long Hottentot skull and the short Bushman skull; very near to the mean of the European group which is presumed to contain both male and female crania. In the analysis of *maximum breadth* the mean for the male Cape Coloured skulls is well below the European group, but above that of the male Bantu. The greatest width is seen in the European group. This confirms the statement made in Martin's text-book that, on arranging groups of crania according to maximum breadth, the widest skulls, with very few exceptions, will be European. On account of the great width, the means for the *breadth/length index* places the European skull highest, next to the Bushman who also tends to brachycephaly, with the Bantu and the Hottentot definitely

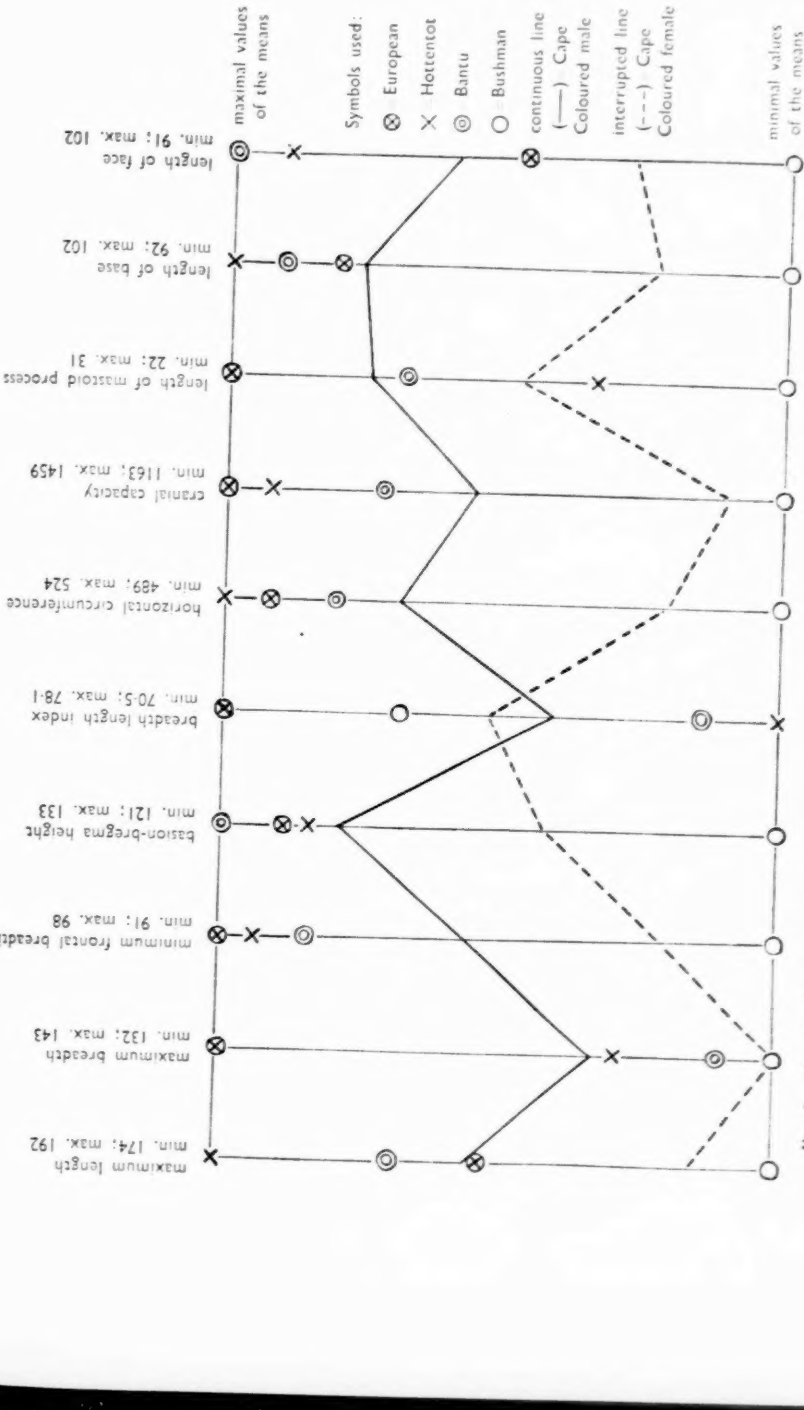

FIG. 1.—Showing the means of certain dimensions and indices of the Cape Coloured male and Cape Coloured female crania, arranged in relation to the maximal and minimal values of the means obtained from the four racial groups used for comparison.

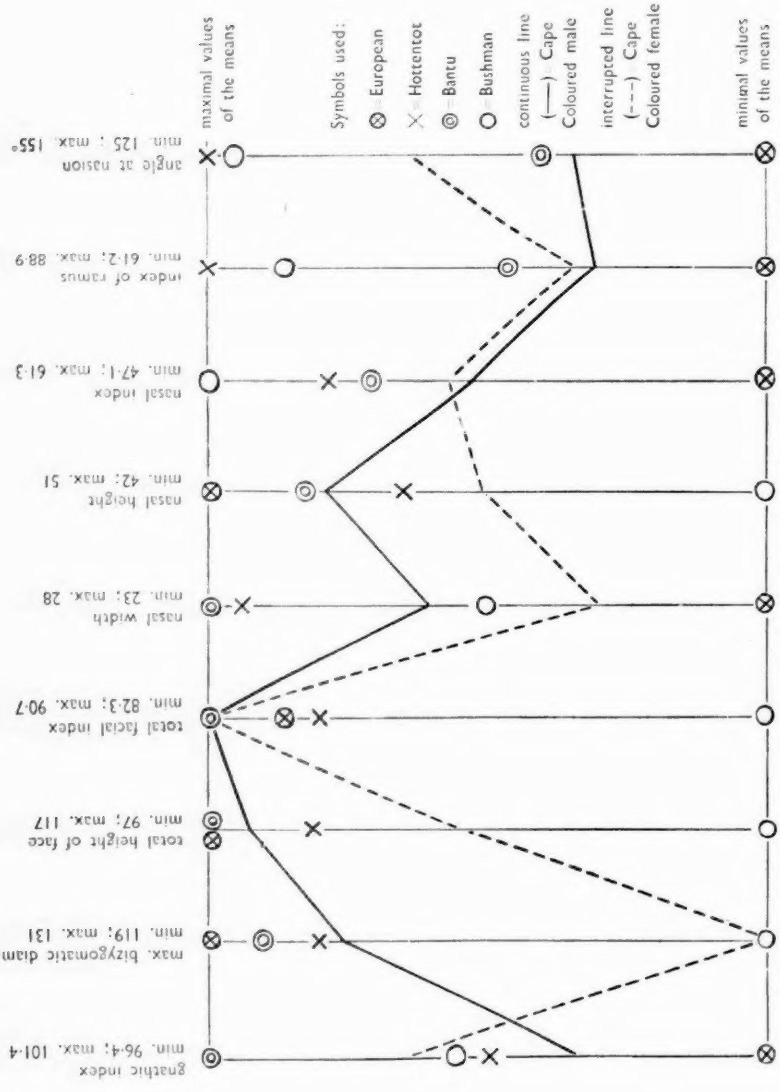

FIG. 2.—Showing the means of certain dimensions and indices of the Cape Coloured male and Cape Coloured female crania, arranged in relation to the maximal and minimal values of the means obtained from the four racial groups used for comparison.

dolichocephalic. The Cape Coloured crania, male and female, come midway, with the European and Bushman on the brachycephalic side and the Bantu and Hottentot on the dolichocephalic side. In respect of *cranial capacity* the mean for the male Cape Coloureds stands about half-way between the maximum and minimum values (fig. 1), the European, Hottentot and Bantu groups all having greater cranial capacities. This can only be attributed to the influence of the Bushman inheritance.

An intermediate position between the means of the four racial groups is maintained fairly consistently, except for the following two dimensions and one index. In *maximum breadth* and *maximum bizygomatic diameter* the female Cape Coloured coincide with the Bushman means. The *total facial index*, for both sexes, coincides with the Bantu, and is also near the European and Hottentot means. A small total facial index differentiates the Bushman from the other groups. The characteristic Bushman skull with its small dimensions for the maxillae and the mandible, has a short face, approaching the infantile type (Drennan, 1931).

On the whole, the hereditary influence of the different racial groups makes itself felt very evenly in the Cape Coloured skull dimensions, without any particular group predominating. This emerges clearly from the general appearances of a representative male Cape Coloured skull (Plate XI). The cranium is neither typically Bantu, nor typically Hottentot; certainly not European, on account of the wide nasal aperture and the rather flattened-nasion region. Also, on the whole, too large and with too long a face to be very Bushman-like. In this particular skull perhaps the Hottentot inheritance shows itself more clearly than that of any of the other three groups, especially as regards the rather flat nasion region (angle at nasion: 134°) and the shape of the mandible (index of ramus: 68·3); the latter tends towards the square-shaped ramus of the Hottentot and Bushman mandibles with their high means for the index of ramus.

Skin Colour and Hair Form.

In the population groups which are here discussed the colour of the skin and the form of the hair are extremely important distinguishing factors, and records of these features were made in each instance when the subjects reached the department; these data can now be related to the skull dimensions and indices in the Cape Coloured. For the skin colour recordings I used von Luschan's colour tablets, and always chose a patch of skin on the inner side of the arm where there is no exposure to sunlight. Many of the colour shades in von Luschan's series are very much alike. After some experimenting I found that nine groups of skin colour shades were sufficient for a satisfactory classification among the Cape Coloured, ranging from the

pinkish white of the European skin (No. 7) through the yellowish, light brown and dark brown tinges to the black-brown of the typical Negro (No. 33). The percentage distribution of skin colour in the whole group of Cape Coloureds (141 male and 60 female adult individuals) is shown diagrammatically in fig. 3 (*cf.* Rhodes, 1945).

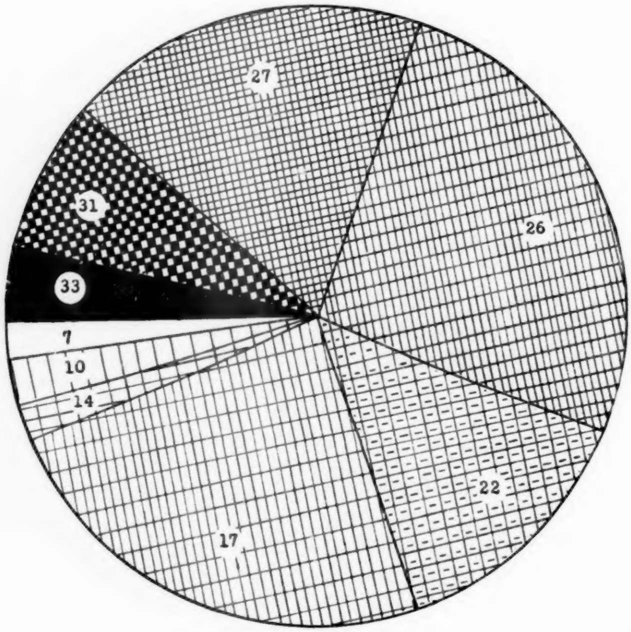

FIG. 3.—Diagram showing the percentage distribution of skin colour among the group of Cape Coloureds whose crania are the subject of the present craniometric study.

In all population groups there is a slight sexual difference in the degree of pigmentation of the skin, the female being slightly lighter than the male (Martin, 1928). The Cape Coloured people form no exception to the general rule, and this fact could be demonstrated most easily by calculating the average position of the males and females among the nine skin-colour subdivisions. The mean for the female group fell about half-way across the No. 22 subdivision, while the mean for the males came about half-way across the next subdivision, viz., No. 26 (*cf.* fig. 3).

As regards *hair form*, it is usual to distinguish three classes: (*a*) the spiral hair, also variously called "frizzy" or "woolly" hair; (*b*) an inter-

mediate class of wavy hair, and (*c*) the straight hair. The majority of the Cape Coloureds studied here had the spiral type of hair (59 per cent.). This is not surprising when we consider that the Hottentot, Bushman and Negro groups all possess the spiral type. Further, anthropologists are generally agreed in considering the spiral hair as dominant over the wavy or straight hair. Among the 59 per cent. are included two individuals where the hair had been noted as "peppercorn", an arrangement of hair seen most typically in the Bushman; "peppercorn" hair means spiral hair arranged in small isolated tufts. Of the remainder, 34 per cent. were classed as having wavy hair and only 7 per cent. had straight hair. The straight hair inherited from the European and Asiatic ancestry certainly behaves as a recessive character.

Correlations.—A dark skin (von Luschan's scale, Nos. 31 and 33) in the Cape Coloureds indicates Negro ancestry and is correlated with spiral hair. On calculation a correlation coefficient of +·72 was found between degrees of pigmentation and spiral hair. This high positive correlation was surprising when one considers that the Hottentot and Bushman peoples also have spiral hair, yet as regards skin colour they are grouped among the yellowish-brown shades (von Luschan's scale, Nos. 22 and 26).

Positive correlations between skull dimensions and degrees of pigmentation could be expected to appear among those features specially characteristic for the Bantu crania. I divided the male Cape Coloured crania into equal parts; one half containing all those classified as belonging to Nos. 7–22 and the other half those belonging to the skin colour subdivisions Nos. 27–33. The dividing line came in subdivision No. 26; these were allotted to either one or other side by chance selection. When the means and standard deviations were calculated separately in the two groups distinguished by their degree of pigmentation of the skin, the results were almost completely negative. The 29 factors appearing in Tables I and II analysed separately showed only slight differences which were insignificant statistically, except in the case of the few dimensions and indices shown in Table IV.

In the darker-skinned group of the Cape Coloured males the length of face and the gnathic index moved significantly towards the Bantu means, while the means of the lighter-skinned group moved towards the orthognathic side and approached the European means (see Tables IV and II). It should be noted that the Bantu or South African Negro is less prognathous than other Negro populations. The mean obtained for the gnathic index in the male Bantu was 101·4. In anthropology text-books (Roy, 1920) the Negro is described as prognathous with a gnathic index above 103.

A significant difference also appeared in the *orbital index*, but is difficult

TABLE IV.—SHOWING THE MEANS OF SOME OF THE DIMENSIONS AND INDICES OF THE SKULLS AND THE CRITICAL RATIOS OF THEIR DIFFERENCES, WHEN THE CAPE COLOURED MALES WERE DIVIDED INTO DARK-SKINNED AND LIGHTER-SKINNED GROUPS.

Dimension or Index.	Group of Cape Coloured Males with Darker Skins.	Group of Cape Coloured Males with Lighter Skins.	Critical Ratio of the Differences in the Means.
Length of base	100·8 ± ·48 mm.	99·5 ± ·52 mm.	1·7 (doubtful significance)
Length of face	99·7 ± ·69 mm.	96·9 ± ·85 mm.	2·5
Gnathic index	99·1 ± ·53	97·3 ± ·59	2·3
Orbital index	77·7 ± ·54	75·9 ± ·54	2·3
Index of ramus	72·5 ± 1·28	69·0 ± 1·22	1·9 (doubtful significance)

to explain when considered in relation to skin colour inheritance. The orbital aperture tends to be narrower from above downwards in the Hottentots and Bushmen, a character associated with the prominent zygomatic bones of these peoples, as against the more rounded orbital aperture of European and Bantu skulls. The darker-skinned Cape Coloured males had a mean orbital index which became very similar to the Bantu mean, but at the same time approached the European mean; while the lighter-skinned Cape Coloured with a lower index (Table IV) approached the orbital proportions of the Hottentot and Bushman (Table II).

A difference in the *index of ramus* means was doubtfully significant, the critical ratio of the differences being just under 2·0. But if it is accepted as significant, the influence of skin-colour inheritance shows itself, in that the mean for the darker-skinned group of Cape Coloured males moved towards the Negroid mean, while that of the lighter-skinned individuals moved towards the European mean. A difficulty arises just as in the orbital index. The Hottentots and Bushmen are intermediate in skin colour, but their index of the ramus is the highest among the four racial groups used for comparison (fig. 2).

The skull dimensions and indices shown in Table IV were the only ones among all the factors appearing in Tables I and II, in which a grouping of the Cape Coloureds into darker- and lighter-skinned individuals showed

significant or possibly significant differences in the means. The coefficients of correlation between skin colour and these factors (except length of face) were also calculated, but the positive correlations were of a low order (Table V). The coefficients of correlation were all in the neighbourhood of +·2, that is for practical purposes hardly any correlation.

TABLE V.—SHOWING THE COEFFICIENTS OF CORRELATION BETWEEN SKIN COLOUR AND FIVE OTHER FACTORS.

	Hair Form.	Length of Face.	Gnathic Index.	Orbital Index.	Index of Ramus.
Skin colour	+·72	+·20	+·22	+·25	+·17

The disappointing results of these calculations for significance and for coefficients of correlation, when the skull data of the Cape Coloured people were related to degrees of skin pigmentation, show quite clearly that genetic skin-colour inheritance is a complex process which apparently does not obey Mendelian laws (Lewis, 1942); all anthropologists are in agreement on this.

In the skin there are two situations where pigment granules can appear: (*a*) in the cells of the stratum germinativum of the epidermis; (*b*) scattered pigment containing cells in the corium of the skin. One or other type of pigmentation may predominate in different races, and thus at least two different genes are involved in skin-colour inheritance.

VARIABILITY IN HYBRID POPULATIONS.

The opinion is often expressed that the crossing of markedly distinct stocks results in population groups which show a specially large variability and frequency distribution curves of an unusual kind, as, for example, curves with more than one peak. The appearance of such a curve was advanced as proving the heterogeneous character of the Cape Coloured people (van Wyk, 1939). The concept that a greater variability of dimensions and indices has a direct bearing on heterogeneity of a type was elevated into the position of a law which is attributed to Boas (Martin, 1928).

The question is of prime importance in anthropological studies, and more recent researches have shown that the older view can no longer be considered as valid. In a discussion on the subject, Trevor (1938) arrives at a conclusion which does not coincide with the genetical assumptions

customarily made in considerations of race crossing. He states that "it is quite clear that most hybrid populations do not tend to be either appreciably more or appreciably less variable than the majority of existing 'unmixed' populations". The author recommends that known hybrid communities should be investigated in this direction, in order to test the validity or otherwise of the older view. The difficulty is that data of the parental populations which have contributed to the hybrid people are seldom available for making comparisons, and it is necessary to compromise by obtaining data of human groups which represent the parent stocks as closely as possible. The manner in which this has been attempted in the case of the Cape Coloureds has been explained above.

When estimating the variability of a set of data the *standard deviations* and the *coefficients of variability* are commonly used (Cameron, 1928). The former gives an idea of the distribution of the data around the mean. The small standard deviation indicates that the observations tend to be heaped around the mean; their "precision" is great, and homogeneity is suggested. The larger standard deviation indicates a wider dispersal of the data around the mean, with a lack of "precision" and a suggestion of heterogeneity.

The coefficient of variability is a measure of the stability of the data, rather than of the character of the distribution; but this coefficient can be used in a similar manner. A small coefficient suggests a homogeneous set of data, a larger coefficient a less homogeneous set.

TABLE VI.—SHOWING THE STANDARD DEVIATIONS AND COEFFICIENTS OF VARIABILITY OF THE FIRST FIVE SKULL DIMENSIONS GIVEN IN THE TABLES, CONTRASTING THE FINDINGS IN THE MALE CAPE COLOURED WITH THOSE IN THE MALE BANTU AND IN THE EUROPEAN GROUP.

	Male Cape Coloured (141 Skulls).		Male Bantu (220 Skulls).		European Group. (186 Skulls).	
	S.D.	C. of V.	S.D.	C. of V.	S.D.	C. of V.
Maximum length	7·0	3·8	6·7	3·6	7·9	4·3
Maximum breadth	5·1	3·8	5·3	4·0	6·3	4·4
Minimum frontal breadth	4·6	4·8	5·1	5·2	4·5	4·6
Basion-bregma height	5·3	4·0	5·8	4·3	6·1	4·5
Horizontal circumference	14·8	2·9	15·9	3·1	17·1	3·3
Totals	36·8	19·3	38·8	20·2	41·9	21·1

In Table VI appear the standard deviations and coefficients of variability of the first five skull dimensions from Tables I and II. The results obtained for the male Cape Coloureds are shown side by side with (*a*) those obtained for the male Bantu; and with (*b*) those obtained from the European group of crania. The male Bantu, *a priori*, might have been expected to show figures indicating a more homogeneous group. But, on the contrary, the standard deviations and coefficients of variability were slightly higher (except for maximum length) than in the Cape Coloured males. The figures for the European crania suggest an even more heterogeneous group: the fact that both male and female skulls were measured may be the explanation.

The cranial dimensions of the Hottentots and Bushmen showed small standard deviations and small coefficients of variability, suggesting a high degree of homogeneity. The explanation was that they were selected groups originally. Skulls that are usually classed as Bush-Hottentot hybrid were not included; only those that showed clearly defined Hottentot or Bushman characteristics. For this reason the data of the Hottentot and Bushman groups could not be used for making comparisons of variability.

The analysis of the standard deviations and coefficients of variability of five unselected cranial dimensions seems to indicate that the Cape Coloureds have become a homogeneous group, and that they are even more homogeneous than the Bantu and European groups which have been used for making comparisons. The data presented in Table VI thus fully support Trevor (1938) in his contention that hybrid peoples, in general, are quite as homogeneous as the so-called "unmixed" populations.

Summary and Conclusions.

1. The Cape Coloured population is defined as a "hybrid" population group, resulting from the admixture of Hottentot, Bushman, European, Asiatic and Negroid racial elements.

2. A group of 201 adult Cape Coloured crania, 141 male and 60 female, were measured according to a standard set of measurements, comprising 17 linear dimensions, cranial capacity, an angle measurement and 10 indices. The data of each dimension, including range, mean and standard deviation, are presented in tabular form, the male and female being given separately.

3. Similar data, covering most of the parent racial stocks from which the Cape Coloured are derived, had been obtained previously, and are presented in a separate table.

4. A comparison is made between the head dimensions of a group of living Cape Coloureds measured by another observer and the present skull

dimensions. The allowance to be made for the soft-part coverings is discussed.

5. The means obtained for the various dimensions and indices in the Cape Coloured crania are compared with the means obtained for the allied racial groups. The position of the Cape Coloured means relative to those of other groups is shown in a diagrammatic manner in two figures. The means of the Cape Coloured male and female crania maintain an intermediate position between the means of the four other racial groups fairly consistently.

6. Skin coloration and hair form among the Cape Coloured are discussed and analysed. It was found that the spiral hair of the Negro, Hottentot and Bushman predominates among the Cape Coloured, and there was a high positive correlation between degrees of pigmentation and the tendency to spiral hair.

7. The Cape Coloured males were divided into two equal groups—one group with darker skins and the other with lighter skins. The differences in the means of the cranial dimensions of these two groups were slight and mostly insignificant statistically, except in the case of certain facial dimensions where the Negro inheritance manifested itself.

8. The variability in hybrid populations is discussed and a test of the variability of the data was made, using the standard deviations and coefficients of variability as criteria. It is demonstrated that the Cape Coloured people are just as homogeneous as two of the parent racial groups.

Acknowledgment.

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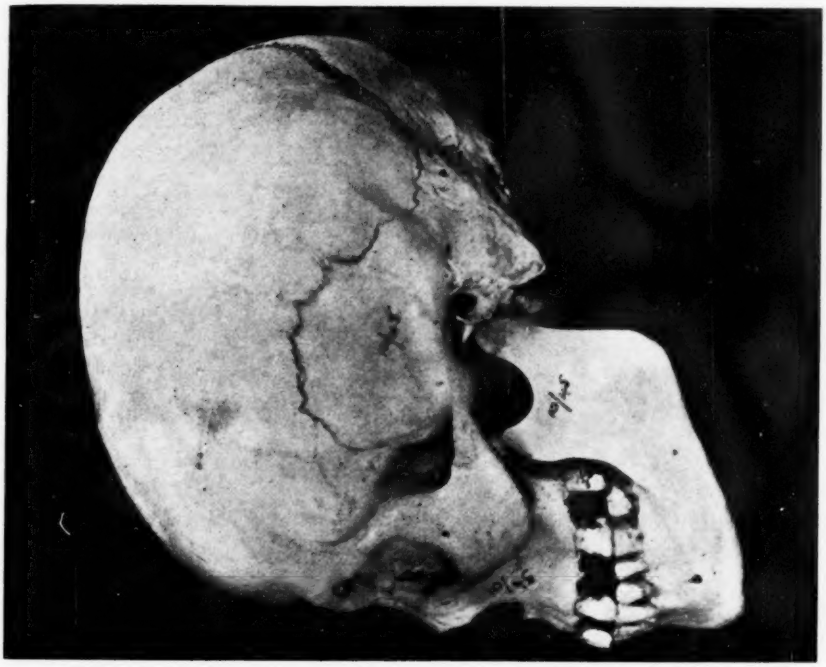

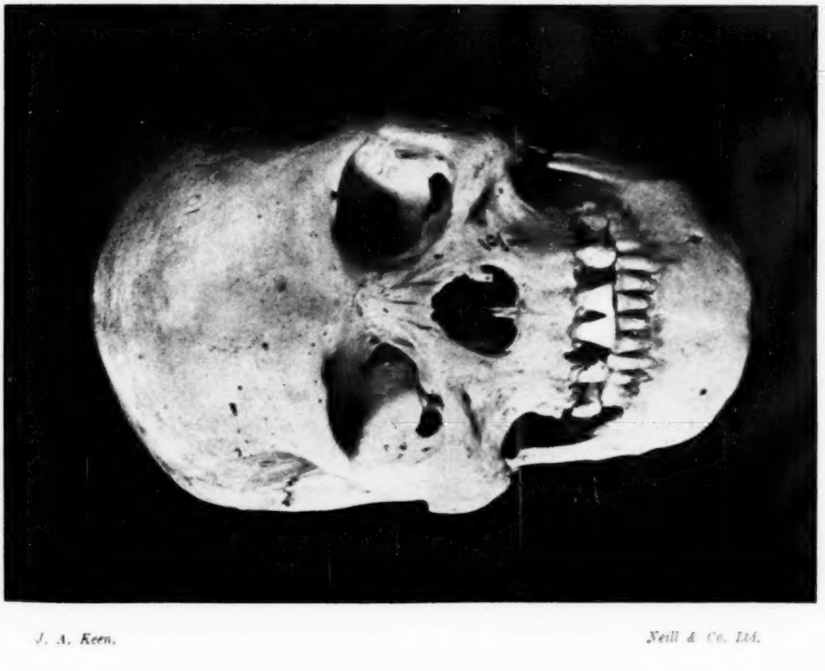

Photograph of the front view and left lateral side view of a representative male Cape Coloured skull.

J. A. Keen. Neill & Co. Ltd.

THE ECOLOGY OF SOUTH AFRICAN ESTUARIES.

Part I. A Review of Estuarine Conditions in General.

By J. H. Day, Professor of Zoology at the University of Cape Town.

(With two Text-figures.)

(Read March 15, 1950.)

CONTENTS.

Introduction.

In the nineteen-thirties Professor T. A. Stephenson and his colleagues made a survey of the animals and plants living on the rocky coasts of South Africa and showed how their distribution is related to the temperatures of the ocean currents. The results of their surveys have been published in a

long series of reports listed in Stephenson (1947). Many members of the original team returned to the Department of Zoology after the war and decided to extend the intertidal survey out to sea and into the estuarine reaches of the rivers. This paper introduces the latter section of the research programme.

The survey is being carried out by a team, and it should be emphasised that although we are agreed as to whom the authorship of the different reports in this series will be credited, we are all responsible for the survey as a whole.

We have now spent over three years on estuarine research in South Africa but we have not published any of our results. We have withheld publication partly on account of the difficulty of getting material identified, partly to obtain records of seasonal changes, but mainly because we wished to gain a wide experience of estuarine phenomena in general before we assessed the peculiar features of any one of them. We also wanted a review of work done elsewhere as a guide for our own work. Obviously lists of species from Europe or elsewhere are not relevant to our purpose, but the physical environment will presumably have the same effects everywhere, and faunistic divisions based on these should have universal validity. Apart from a necessarily brief chapter in Yonge (1949) there has been remarkably little general discussion about estuarine conditions, although the list of references at the end of this paper show that many isolated problems have been tackled. This paper contains a discussion of these problems, with additional evidence from our own work in South Africa, and serves as an introduction to the reports on individual estuaries which will follow in this series.

We have received financial support from four main sources which we now gratefully acknowledge. The cost of the major items of equipment, totalling £900, has come from part of a block grant made by the Carnegie Corporation of New York to the University of Cape Town. With this we have bought a one-ton motor-van and converted it into a caravan-cum-laboratory complete with collecting gear, test equipment, boxes of preserving jars, outboard motor and all the many small items needed when working hundreds of miles from our Cape Town base. The South African Council for Scientific and Industrial Research are contributing the salary of a full-time research assistant so that the field work is not limited to the university vacations. The Staff Research Fund of the University of Cape Town has made several grants, totalling £300, to cover special equipment and investigations near Cape Town. But the main expense in survey work is the running cost of the expeditions themselves, many of which involve the transport of parties of six or eight biologists over hundreds of miles and lasting three or four weeks at a time. The cost of surveying the Natal

estuaries is being met by a generous grant of £1000 from the Natal Provincial Council, but further sums must be obtained if we are to complete the Cape section of the work.

This type of ecological work cannot be done without the help of a large body of systematists, particularly in South Africa where much of the fauna is unknown. We would like to take this opportunity of thanking the many specialists who are helping us. These are at present: Mr. Burton of the British Museum (Sponges), Dr. Stephen of the Royal Scottish Museum (Gephyrea), Professor O'Donoghue of Reading University (Polyzoa), Dr. Barnard of the South African Museum (Crustacea, Pycnogonida), Miss Clark of the British Museum (Echinoderms), Dr. Rehder of the U.S. National Museum (Pelecypod and Gastropod Mollusca), Dr. Ranson of Paris (Oysters), Dr. Eales of Reading University (Opisthobranchs), Mr. Rees of the British Museum (Cephalopods), Dr. Zinn of Rhode Island State College, U.S.A. (Tunicates), Professor Smith of Rhodes University College, Grahamstown, South Africa (Pisces).

Our list of systematists is still incomplete, but it may be noted that the Polychaeta, Birds, and Cirripedes and Hydrozoa are being identified by J. H. Day, G. J. Broekhuysen and N. A. H. Millard respectively, all of the University of Cape Town.

The Geography of an Estuary.

The Limits of an Estuary.—There are many references to work on brackish-water faunas of the Baltic Sea, the Norwegian fjords, the Zuider Zee, the Bristol Channel and Severn Estuary, "the marine estuary of Elkhorn Slough," and others, so it is important to define the limits of an estuarine area. The dictionary definition is quite straightforward as "that area in a river in which tidal effects are evident." But the mere rise and fall of water-levels has little effect on the fauna, and most estuarine surveys neglect the upper freshwater reaches of an estuary. The main characteristic of an estuarine population is its ability to tolerate *changes* in salinity; usually these changes occur within the lower reaches of the river, and what is said here about estuaries is meant to apply only to the parts of river systems where there is an appreciable variation in salinity due to the sea. With Yonge (1949) we have excluded areas where the mixing of salt and fresh water takes place beyond the river-mouth, as happens at the bottom of a waterfall or outside a large and powerful river such as the River Plate, and also areas where the salinity is stable even if it is appreciably less than normal sea-water. On the other hand, the omission of any reference to tides allows us to include those blind estuaries where the salinity varies from less than sea-water in the rainy season, through the sea-water range

when the estuary bursts open to the sea, to well above sea-water values in the dry season. There are many such estuaries in South Africa because the smaller rivers are often cut off from the sea for several months by sand-bars, and rapid evaporation then boosts the salinity to high values.

The Shape of the Estuarine Basin.—When a young river flows down to the sea it cuts its own channel, whose depth, width and shape will depend on the volume of the river, the slope and the nature of the rock-bed. In areas of submergence the sea will invade more and more of the valley until a deep "drowned valley" is formed; in areas of emergence the river cuts a deepening channel between ravine-like banks. In either case the original shape and depth will be modified by the silt brought down by the river, the range of the tides and the amount of wave action. In the Mediterranean, where the sea is relatively calm and the tidal range negligible, the estuaries gradually broaden towards their exits, and deltas are common. In England, where tidal action is considerable and wave action moderate, many estuaries broaden and tidal mud-banks appear, but the main channels are kept open by the outflow of the river assisted by tidal currents. In South Africa, where wave action is usually extreme and tidal range seldom more than five feet, a sand-bar is rapidly built up at the mouth, behind which the estuary spreads out as a wide, shallow lagoon. During the dry season the tidal action alone may be insufficient to keep the channel open and the estuary may become blind (*i.e.* cut off from the sea). Krige (1927) states that the South African coast is "typically a young to mature coast-line of submergence modified by later emergence phenomena;" and of the rivers: "Although not recognisable from the map as such, practically all the South African estuaries are true drowned valleys more or less silted up." He also describes the origin of the bars and their effects on silting: "The presence of beach-bars periodically and sometimes almost permanently closing the majority of our estuaries must, by preventing escape, assist materially in the silting-up of the lagoons as Rogers has postulated. These bars have been built up by waves mostly at bay-mouth bars, *i.e.* as bars jutting across the 'bay' or river estuary from the adjacent promontories, the sands being derived from their eroded portions by longshore currents."

The Effect of the Shape of an Estuary on the Physical Environment and on the Fauna and Flora.—The shape of the estuary is of basic importance. If the mouth is wide and deep and the banks form a tapering funnel, the tides will extend high up the river and a bore may develop as in the Severn. This will be elaborated in the next section on "Currents". If the mouth is deep but constricted and wave action in the sea outside is moderate, a vertical salinity gradient may develop as in the Tamar and the Tees. If

in addition to the vertical salinity gradient there is a submarine sill, the heavy saline water at the bottom of the estuary may become stagnant and anaerobic conditions may develop as in some of the Norwegian fjords. If the sill is very shallow, it may accumulate sand by wave action until the mouth closes completely. The estuary then expands behind this sand barrier into a broad lagoon in which the salinity, substratum and current systems are entirely altered. These effects are all considered in greater detail under the relevant headings.

But apart from these indirect effects, the depth at the mouth has its own direct effects on the constitution of the estuarine fauna. If the mouth is very shallow the larger fishes will not enter the lagoon, and the closing of the mouth will prevent the movement of all animals to and from the sea. Most estuaries burst open during the rainy season, but some remain closed for several years. The initial fauna then depends on which larval or juvenile forms are introduced at the time of closure. Those with short lives will disappear unless they can breed in the estuary. Others will die because the salinity and other physical factors are modified by rain or evaporation. Blind estuaries usually have poor faunas, but occasionally they have a rich vegetation.

The Physical Environment.

Wave Action.—One of the most obvious differences between an estuary and the open sea is the decreased wave action. Where the mouth is wide, waves penetrate into the entrance; where the mouth is constricted the change is very sudden. Many workers, including Stephenson (1947), have shown how greatly wave action may influence a fauna. In Britain, where wave action along the coast is not intense, the effects are quite obvious: in South Africa, where practically the whole length of the coast is subject to the full force of oceanic swell, even a minor headland makes a marked difference to the fauna, and when one walks from an open shore inland along the banks of a sheltered lagoon the change is most striking. Of course it is difficult to disentangle the effects caused by changes in salinity and substratum from those due to wave action, but it can be done by comparing the fauna of an estuary with those of an open shore and a sheltered inlet in which there is no reduction in salinity. This work is in hand, and preliminary results already show that remarkably few of the common shore animals occur either in estuaries or in sheltered inlets. In Britain, where many of the shore animals extend into the mouths of estuaries, even small variations in shelter have their effects, and Beanland (1940) has drawn attention to their importance.

The Current System.—The main currents in an estuary are due to the

inflow from the river and the rise and fall of the tides. Before the complexities within the estuarine basin are considered it is as well to review the variations of the currents which enter it. The strength of the river-flow depends on the slope of the channel and the volume of the water it contains, which increases after the rains and may fall to *nil* during a drought. The strength of the tidal currents entering the mouth of an estuary depend on the tidal range, the volume of the estuarine basin and the size of its mouth. The tidal range varies from neaps to springs, but the presence of an on-shore or off-shore wind modifies the tidal range considerably. Over any tidal cycle the current strength increases from *nil* at high or low water to maximum velocity about three hours later.

Within the estuary basin the river-flow and the tidal range produce complex and variable currents. While the tide is rising, the sea attempts to flow into the estuary and the river water attempts to escape. If a vertical salinity gradient exists, the lighter river waters may flow out at the surface while the heavier sea-water enters below, and Hartley and Spooner (1938) have shown that, farther up, the opposing currents may both be visible at the surface. They say of the Tamar estuary: "When much fresh water is coming down, the flood tide will move to one side of the river before its influence reverses the direction of flow on the other." If the sea and river waters mix so that no salinity gradient exists, the rising tide will reverse the normal flow of the river and move up the estuary, but since the two currents are in opposition, the movement is relatively slow, and eventually stops at high water. During the ebb the river-flow reinforces the out-flowing tide, and the maximum velocity is observed at mid-tide. The velocity then gradually decreases and may stop at low water. The velocity is not uniform across a section of the estuary; the swiftest currents are at the surface in the centre of the channel and from here the strength decreases towards the bottom and towards the banks, and particularly towards the intertidal shallows. The fact that water movements over the upper tidal flats between neap and spring high-water mark are very slow has important consequences on the grade of the substratum and thus on the distribution of the estuarine fauna.

Although the duration of a complete tidal cycle in an estuary is the same as that in the sea, the duration of the ebb is greater than that of the flood, so that the time of low water at the head of an estuary is later than it is at the mouth. In the enormously long estuary of the Amazon, where the tidal wave has only penetrated to the lower reaches before the next one arrives at the mouth, there are said to be eight tides along the length of the estuary. Bassindale (1943 *a*) has also shown that, in the Severn, the volume of sea-water which enters during high spring tides does not have time to escape before the next tide starts rising at the mouth, and for this

reason the neap tides expose more of the estuary bed in certain stretches. The same phenomenon occurs in the Kosi Bay estuary on the Zululand coast of South Africa, while in the Knysna estuary of the Cape the lowest tides occur two days before springs and two days after. The even more complicated effects of double tides on the Californian coast are described by MacGintie (1935).

The strength of the currents within the estuary are determined by the shape of the basin. Where it is broad they are slow and where it is constricted they are rapid. If, as often happens, the estuary gradually broadens towards its mouth, the outflowing river currents gradually decrease; but the incoming tidal wave is gradually constricted by a funnel-like basin and may develop into a bore such as that in the Severn described by Bassindale (1943 *a*). Here the tidal range has a maximum of fifty feet and is accompanied by rapid and turbulent currents which increase the turbidity and have a marked effect on the fauna. If the estuary consists of a river which opens into a broad shallow lagoon with a constricted exit to the sea (roughly onion-shaped), the river currents lose their force at the head of the estuary and the tidal currents are feeble except in the channels at the mouth, so that the broad middle reaches of the lagoon are very calm.

The distribution of strong and weak currents in an estuary has been considered in detail because they have such important effects on estuarine faunas and floras. This has been emphasised by Bassindale (1938) for the Mersey, and Spooner and Moore (1940) for the Tamar. But the current system affects so many other factors of the physical environment such as turbidity and substratum that its own direct effects on the biota are difficult to disentangle. The indirect effects will be discussed later under the appropriate headings. The direct effects of currents on estuarine faunas have not been studied in detail, but recently Bassindale *et al.* (1949) have started a programme of research on the effect of currents on marine animals and plants. In the absence of any work on the direct effect of estuarine currents it is only possible to suggest certain features of particular interest. One of the most important of these is the transport of the planktonic larvae from the sea high up the estuary. This is not obvious in an open estuary, but when an estuary has been closed for some time the fauna becomes impoverished, and when it regains contact with the sea and the larvae which have been swept in by the tidal currents become established, the change in the fauna is very marked. This has been observed in the periodically blind estuary of the Klein River near Hermanus in South Africa. From the changes in the fauna it would seem that many estuarine animals have comparatively short lives and must be continually recruited from the sea. A second important effect of estuarine currents is that they carry more water to the sea than returns with the flood-tide. This means that plankton

is being continually lost to the sea and is not so important in the economy of an estuary as it is in the sea. The species which do occur spend most of their time on the bottom and only appear in the surface catches during the night.

Turbidity.—Estuaries are notoriously more turbid than the sea. The suspended matter may be eroded from the land and brought down by the river; it may be eroded from the estuary bed itself or swept in from the sea. The important factors are erosion, transportation and deposition, and, as noted previously, these are all reversible processes depending on the strength of the currents.

In countries like South Africa which is subject to periodic droughts, the degree of soil erosion and consequent turbidity and silting of rivers and estuaries present very serious problems. As far back as 1927 Krige reported that: "Owing to veld deterioration by overgrazing in the Karoo, as pointed out in the Union's Drought Commission Report, the southern rivers are more intermittent, but much more muddy when in flood, and for this reason the silting up of estuaries may now proceed with increasing rapidity." This prophecy has proved only too true. The suspended silt is carried into the estuaries as a dark brown flood which fills the whole basin and continues out to sea for many miles as a muddy stream. This has been observed all along the Natal and Transkei coast.

The foregoing is an extreme picture of what can happen when periodic droughts are followed by floods. Normally erosion is a slow process and only fine silt is deposited in the upper reaches of an estuary. The colloidal particles are first coagulated by the electrolytic effect of salts and then settled in the slower currents. Sverdrup *et al.* (1942) state that: " . . . fine-grained material, when mixed with sea-water, tends to flocculate into units which settle with a velocity equivalent to that of quartz spheres between about 5 and 15 microns in diameter, that is they settle between 1 metre and 20 metres per day."

But fine silts and clays are not the only colloidal particles carried down by rivers. It has often been observed that even quiet moorland streams are coloured by peaty matter. The dark colour is said to be due to the decomposition of vegetable matter, particularly pollen. The colouring matter is a positively charged colloid and is deposited in the presence of colloidal silt which is negatively charged, but it is not coagulated by the metallic ions in sea-water, and in some South African estuaries, such as the Klein River estuary at Hermanus, the brown colour persists even in salinities of 30 parts per thousand.

The next source of turbidity and suspended silt is the erosion of the estuary bed itself. This is particularly important in the Severn, and Bassindale (1943 *a*), who worked out the distribution of silt in detail, states

that: "It has been assumed that the zone of turbid water is a function of the shape and the current system of the estuary. . . ." The zone of maximum turbidity is in the middle reaches where the tidal currents are strongest, and the amount of silt in suspension increases from neap to spring tides. Usually the maximum turbidity is observed in the narrow channels where the currents are strongest. But this is not always the case. Where river and tidal currents are absent the only water movements are those due to the wind, which is most effective over wide stretches of shallow water. Thus in the broad shallow parts of Lake St. Lucia on the Zululand coast the waves stir up a lot of silt from the bottom, and the clearest water is found in the deeper and narrower channels.

The Penetration of Light.—The amount of suspended matter determines the penetration of light, and turbidity can be measured by a Secchi disc. Where the quantity of silt is large a direct method of determining the weight of silt per unit volume of water can also be used, and Francis-Boeuf (1943) gives a table of the relation between Secchi disc measurements and the weight of sediment per unit volume. This is summarised below.

State of Tide.		Low water.	5 hrs. to H.W.	4 hrs. to H.W.	3 hrs. to H.W.	2 hrs. to H.W.	1 hr. to H.W.	High water.
Silt content in gms./litre	Surface	0·27	0·26	0·22	0·13	0·11	0·18	0·19
	Bottom	0·39	0·36	0·32	0·24	0·19	0·26	0·21
Transparency measured by Secchi disc in metres		0·35	0·35	0·45	0·60	1·0	1·0	1·4
Salinity per thousand		23·8	24·2	30·0	32·0	35·0	33·6	34·0

In practice it has been found that if a Secchi disc can be seen at a depth of one metre, the quantity of silt is too small to be determined accurately by direct methods.

Cooper and Milne (1938) have described an exact method for determining the penetration of different wave-lengths by the use of a Zeiss Pulfrich photometer, and have shown that the relative penetration of different wave-lengths in a turbid estuary is different from that found in clear sea-water. They state: "In water, therefore, the region of optimum transmission will result from two opposing factors—absorption by suspended matter cutting out the blue and green, and absorption by the molecules of water and the dissolved salts cutting out infra red and much of the visible red." They note further that Petterson, Hoglund and Landberg (1934)

have suggested that the compensation intensity at which photosynthesis just balances respiration by diatoms is about 400 lux. While other important estuarine plants such as *Zostera* and *Enteromorpha* may require different values, it would be of great interest to link up lux values with Secchi disc measurements and the weight of sediment per unit volume.

The Effect of Turbidity and Silt on the Estuarine Community.—High turbidity has a twofold effect on the estuarine community. Muddy water obviously limits the depth at which photosynthesis can take place and thus limits the basic supply of plant food. Thus Cooper and Milne (1938) have shown that turbidity compresses the zonation of plants. This has been confirmed by Milne (1940) working on the plant and animal communities of buoys, and he further suggests that the red algae are favoured at the expense of the brown. Milne's suggestion receives confirmation from our observations in South Africa, and we have noted that in the turbid waters of the Berg River estuary *Zostera* is limited to the intertidal banks, whereas in the clear waters of the Knysna estuary *Zostera* extends at least three feet below low-tide mark. It has also been suggested that certain types of animals do not grow in muddy waters. Milne (1940) found no evidence of this, and says: "It is sometimes suggested that animals with delicate ciliary or pore mechanisms (suspension feeders) will be limited by suspended silt . . . on the Tamar buoys, just as in the bottom fauna of the Tees, Tay and Tamar estuaries (Alexander *et al.*, 1935) there is no marked difference between the penetration of the two groups." In spite of this, the matter is still controversial, and Yonge (1949) quotes work by Purchon to show that many suspension feeders which are absent from the turbid waters of the Bristol Channel are present in the clearer waters of a dock.

The second effect of silt is its actual deposition as soft mud. Where this occurs slowly a limited mud fauna exists, but where the deposition is rapid both plants and bottom-living animals are smothered. This has happened in at least two large estuaries in South Africa, the Umzimvubu and the St. Lucia. The St. Lucia estuary is joined near its mouth by the Umfolosi River whose swamps have recently been canalised, so that the soil eroded in the upper reaches now passes as a chocolate stream directly into the mouth of the St. Lucia. With the rising tide this muddy water is carried back up the St. Lucia estuary and is so dense that a Secchi disc of 6 inches diameter is invisible below 2 inches. Enormous banks of soft glutinous mud are being deposited, and *Zostera*, which according to reports was once common, is now absent and the only algal growth is a thin film of *Enteromorpha*. Benthonic animals are scarce and mainly restricted to the upper tidal levels. Higher up the St. Lucia, beyond the range of the Umfolosi mud and also near the mouth of the neighbouring Richards Bay estuary, *Zostera* is abundant and benthonic animals are plentiful.

The Substratum.—It has been shown that the original rocky channel cut by a young river is later silted up by material carried down from the land or washed in by the sea. It has also been noted that the arrangement of these sediments in the estuary is a function of the shape of the basin and the current systems. In young rivers where the bed slopes steeply and the river currents are strong, erosion is still an active process and the estuary bed is mainly rocky, with finer pebbles, gravels and sands at the mouth. In mature rivers, with broader basins and wider mouths, the strength of the river current decreases at the head of the estuary and the suspended silt is gradually deposited. It may be eroded again, sorted and redeposited many times until the grade of the soil conforms to the current system previously discussed. In general, there is a gradation of particle size along the length of the estuary from fine muds in the upper reaches to coarse sands at the mouth.

There is also a vertical gradation of particle size in relation to the varying strength of the currents at different states of the tide. For the same reason the slope of the banks is not uniform and tends to flatten out above mid-tide level. Thus there are usually extensive mud flats near the high-tide mark and steeper banks of sandy mud towards the low-tide level. Variations in current strength, in narrow channels and back waters modify this general picture. The distribution of sediments in the Tamar is discussed by Hartley and Spooner (1938) and Spooner and Moore (1940), and the latter find a similar distribution in most English estuaries. In the lagoon type of estuary where a small river feeds a broad shallow lagoon with a narrow exit, the differences in current strength will be more marked but the arrangement of sediments follows the same general pattern. However, local waves within the lagoon will not allow the finer muds to settle on the beaches, and the foreshore is often clean sand. Even in blind estuaries the pattern is similar, for the sands at the mouth are well scoured whenever the mouth is open and the river muds are deposited high up the estuary.

The Effect of the Substratum on the Fauna.—There is no doubt that the substratum has a very profound effect on the constitution of the fauna and the distribution of the component species. Rocky areas are commonest at the mouth, and rock-loving species are largely limited to this section of an estuary, though they will also occur on the piles of bridges and wharves, buoys, and in tropical countries on the roots and trunks of mangroves as shown by Fischer (1940). But even in these situations the fauna is scanty, possibly because, as Percival (1929) has remarked, the surfaces are covered with a thin film of mud "which is lifted at the flow and redeposited at the slackening of the tide." However, the rocks and other solid objects are important in providing shelter for the many creeping animals, and although

an isolated muddy rock may bear few attached forms, numbers of creeping forms will be found hidden beneath it.

The fauna of gravels and clean, coarse sands near the mouth of the estuary is also limited, because the sandbanks are unstable and do not permit the construction of open burrows and also because they contain little detritus food. Again, as noted (Percival, 1929), the soft slurry muds of the upper reaches ". . . generally carry a poor macrofauna," and this is largely restricted to the surface, presumably because of the oxygen lack in the lower layers. Thus the richest parts of the estuary are the banks of muddy sand, particularly those overgrown by *Zostera* which provides shelter for small surface forms. In these there is sufficient fine silt to allow the construction of permanent burrows, and sufficient detritus to provide a rich supply of food.

Both Beanland (1940) and Holme (1949) have analysed the faunas of muddy sand and show that there is a close relation between the infauna and the grade of soil. Beanland discusses methods of soil analysis and shows that the percentage of fine grain material is one of the most important features. Holme made a detailed analysis of the fauna of the intertidal banks near the mouth of the Exe estuary where "measurements of salinity, temperature, pH, currents and wave action show that these are similar for all stations" so that "it has been possible to observe the distribution of the fauna in relation to type of soil without the usual complications due to differences in other factors."

Holme found that clean, coarse sand had the poorest fauna while muddy sands (*i.e.* mixtures of sand and silt) had much richer faunas. The correlation between animal distribution and silt was obscure, and suggested methods of action were: "(i) a direct effect of silt upon distribution; (ii) an indirect effect of silt, through its effects on the type of vegetation, consistence of the soil, drainage, or some chemical or physical factor in the soil; (iii) some other factor of which silt may be merely the indicator. With regard to the last, the organic content of the soil is probably closely related to the quantity of silt,since both fine organic matter and silt tend to settle in the more sheltered parts of an estuary. In grade analysis, much of this organic matter will be represented in the silt fraction, though it would appear that in the samples dealt with here much of the silt was of inorganic origin."

Two of the suggested methods of action of silt deserve further discussion. The first is drainage and the second is organic content. Holme shows that differences in drainage are related to changes in the burrowing fauna, so that in a well-drained sand the worm *Ophelia bicornis* is present, whereas in a water-saturated sand it is replaced by the bivalve *Tellina tenuis*. Differences in the vertical zonation of a sandbank are explained on this same basis

of drainage. With regard to the second point, the organic content, MacGinitie (1935) has drawn attention to the predominance of detritus feeders in Elkhorn Slough, Beanland (1940) discussed the matter further, and an analysis of Holme's own data shows that from mid-tide down, where the percentage of silt and clay increased from 1·6 per cent. at station II to 11·2 per cent. at station VI and 16·6 per cent. at station IV, the greatest weight of burrowing animals "was made up of only four species, *Arenicola*, *Scrobicularia*, *Cardium* and *Ampharete*." All of these are detritus feeders, *Arenicola* being a "soil-swallower" and the others selecting organic particles from the surface layers. The significance of the organic content of silt appears to be clear.

The Salinity.—An estuary has been defined as that part of a river system where there is an appreciable variation of salinity due to the sea. This emphasises that estuarine waters are essentially brackish, that the concentration of salts is variable and that the composition of the dissolved salts is essentially similar to that of the sea. Though a few rivers carry an appreciable amount of salt in solution, the vast majority carry so little that for biological purposes it is justifiable to assume that the salt content of estuarine waters is marine in origin and the salinity can be determined by a chloride titration in the same way as sea-water. This point is discussed by Howes (1939), who describes methods for the estimation of the major ions.

The salinity in an estuary usually increases from very low values in the river water at the head of the estuary to about 35 per thousand in the sea at the mouth. Exceptions will be noted later. At any point in the estuary the salinity increases with the rising tide and is greater at springs than at neaps. Evaporation during the dry season (which does not always coincide with the summer) raises the concentration still further. The vertical and horizontal distribution of salinities along the length of an estuary are very complex and are best discussed in relation to the different types of estuaries.

Open Estuaries without Vertical Salinity Gradients.—The simplest case is that found in large estuaries such as the Severn which has been so completely described by Bassindale (1943). In this estuary the strong, turbulent currents prevent the formation of vertical salinity gradients so that the sea-water and the brack water are thoroughly mixed at the mouth and the salinity gradually decreases towards the head of the estuary. At spring tides a greater volume of sea-water enters at the mouth, so that the salinity at any particular point is higher and the region of brackish water extends farther up the river. The reverse is true at neaps. In the rainy season more fresh water flows down from the river, so that the brackish water region is more restricted and the salinity at any particular point is lower. So much for the horizontal distribution of salinity up and down the estuary.

Although there is no vertical salinity gradient in the water it will be appreciated that the banks, which are only covered by the highly saline waters of the high tide, are subject to a higher and more stable salinity than those at the low-tide mark and below, which are subject to high salinities at the flood and low salinities at the ebb, and thus have a lower and more variable salinity. These differences may be important in the distribution of intertidal animals, but this has still to be proved.

The above remarks refer to water above the substratum, but Reid (1930) has shown that the salinity of water within sand is not necessarily the same as that of the overflowing water. He says: "It would seem that a stream of fresh water flowing over intertidal sand has little effect on the salinity in that sand to any great depth." Alexander, Southgate and Bassindale (1932) found similar conditions occur in a muddy substratum, and further work on the same subject has been done by Nicol (1935). All these researches draw attention to the fact that the salinity is very stable a few inches below the surface. Nicol goes on to show what happens when a salt-marsh pool dries up completely. The sequence of changes depends on the type of substratum, and there is a great difference between stiff mud and porous sand. In the former the surface inch becomes very saline and eventually dries and cracks, while the lower layers show relatively small increases in salinity over the same period. In sand, drying and consequent increases in salinity proceed to a much greater depth and there is not the marked difference between the surface and the lower layers.

Estuaries with a Vertical Salinity Gradient.—Two examples of this type of estuary have been described in detail: the Tees by Alexander, Southgate and Bassindale (1935), and the Tamar by Milne (1938). In these the incoming salt water from the sea does not mix completely with the river water, which is lighter and floats on the surface so that the salinity increases with depth. It would appear that, in the absence of turbulent currents, the heavier sea-water starts to flow in along the bottom as soon as the tide starts rising, while the lighter river water is still flowing out on the surface, but Hartley and Spooner (1938) state that in certain stretches of the Tamar the saline water may move up one side of the channel before the outflow is reversed on the other. Eventually the outflow of the river stops and sea-water enters up the whole channel.

The main outflowing and inflowing currents are restricted to mid-channel, and Milne (1938) has shown that on a falling tide, as the less saline water flows out, the isohalines bulge downwards in mid-channel, while on a rising tide, as the more saline sea-water enters along the bottom, the isohalines bulge upwards in mid-channel. This means that the greatest changes in salinity are restricted to the centre of the channel and do not affect the animals living on the bed or the banks of the estuary except at the low-tide

mark. Few animals live on the bed of an estuary and ". . . the higher the level in the intertidal area at which an organism lives the more favourable the salinity conditions it will meet" (Milne, 1938).

Vertical salinity gradients are best marked where currents are weak and deep troughs occur in the estuary bed. The presence of sills at the entrance of some Norwegian fjords thus prevents mixing except in the surface layers, and the bottom water is highly saline, stagnant and lacks oxygen. Preliminary investigations in Kosi Bay on the Zululand coast indicate that vertical salinity gradients also exist in some of the chain of lakes which form that estuary.

Blind Estuaries.—While such estuaries are open, the salinity distribution is quite normal and there are the usual tidal changes. But as soon as the bar closes, tidal effects disappear and the only salinity changes are slow ones due to three opposing factors. The salinity may slowly decrease as the estuary receives more fresh water from the river or from rain and the saline water at the seaward end slowly seeps out through the sand-bar. Or the reverse may happen. If evaporation exceeds the inflow from the river and the seepage through the bar, the salinity may slowly rise until the estuary becomes much more saline than the sea. In extreme cases parts of the estuary may dry out completely and form salt-pans. Sooner or later the rains come, the estuary fills up and either bursts its own way to the sea or has an artificial channel cut for it by the farmers whose lands along its banks are being flooded. The salinity changes at this time are very sudden and very drastic. Every variety of blind or temporarily blind estuary is found in South Africa, and a description of one will form Part II of this series on "The Ecology of South African Estuaries."

Estuaries with Reversed Salinity Gradients.—The estuaries described so far all have a normal distribution of salinity and vary from fresh water at the head to sea-water or very saline water at the mouth. But this distribution may be reversed so that the salinity increases from the seaward end to the upper or more isolated reaches. This happens where evaporation exceeds inflow from the river and the mouth is shallow so that there is little exchange with the sea. The water at the mouth which is washed in and out by the tides remains the same salinity as the sea, and the salinity gradually increases towards the upper parts of the estuary. This was found to occur after a prolonged drought in the St. Lucia estuary in Zululand. The upper reaches form a series of broad shallow lakes at the same level as the sea. After the prolonged drought the rivers were barely flowing and the freshwater inflow was not sufficient to compensate for the evaporation in the shallow lakes so that the losses were made good by an upflow from the sea. By the summer of 1948 the salinity in the uppermost lake had risen to over 50 per thousand, farther down it was less than 40 per

thousand and near the sea it was 35 per thousand. The whole salinity distribution was reversed by floods during April 1949, and by July a normal salinity gradient existed.

A reversed salinity gradient has also been described by Hedgpeth (1947) in the Laguna Madre of Texas. This lagoon appears to be a relatively isolated portion of the main estuary, with a small freshwater inflow and a very shallow exit to the sea. Strong currents are absent, evaporation is rapid, and salinities of 90 per thousand or over occur in the upper reaches, but nearer the sea-exit the salinity decreases to sea-water values. Hedgpeth gives an illuminating account of the salinity exchanges between the heavy saline water of the lagoon and the lighter sea-water entering with the tides. He says, " . . . salinity exchange is a lateral and laminar process and is not effected in or through narrow channels. . . . In order to be effective even within the limits of hydrographic conditions, a channel must slope down in the direction of the less saline body of water (the sea) so that the denser water will flow into the less saline basin. If the channel bottom is level or has a higher threshold nearest the lighter water, the denser water will not move out. Even under optimum conditions the incoming current of lighter water in the upper layer will pick up some of the heavier water below it and therefore be of higher salinity than the water from which it originated." Hedgpeth also shows that a natural constriction prevents effective exchange between two parts of the lagoon so that it is divided into two salinity regions. His observations on salinity exchange in hypersaline estuaries has been quoted at length because it is felt that similar conditions exist in many arid areas. The case of St. Lucia estuary has already been mentioned, and it is probable that there are other hypersaline lagoons on the west coast of South Africa.

The Rate of Change of Salinity.—So far only the distribution of absolute salinities in estuaries have been considered. But the rate of change is also important. Bassindale (1943 *b*), by way of introduction to a very comprehensive account of the rate of change of salinity, says: "It has long been known that if the salt content of the water in which they are living is changed sufficiently slowly, many animals can acclimatize themselves to large changes. Thus although the magnitude of the change is important, the rate of change is also significant."

The most obvious changes are those due to the tides. An animal on a particular bank may be subjected to (say) 15 per thousand salinity at low tide and (say) 27 per thousand at high tide, a change of 12 parts per thousand or 12 grams of salt per litre over a tidal cycle of about 6 hours. But the duration of the flood-tide or the ebb varies along the length of the estuary, so that it is necessary to follow Bassindale's example and express the rate of change in grams of salt per litre per hour (g.p.l.p.h.).

In the example quoted above the rate is 12 grams per 6 hours or 2 g.p.l.p.h.

Bassindale has also shown that because the tides and the salt water do not always extend the same distance up the estuarine channel, the maximum salinity change per tide does not necessarily give the greatest rate of change per hour. Thus in a certain stretch of the Severn the rate of change per hour is 15 g.p.l. "In the Tees the maximum salinity change per tide is much greater than in the Severn, amounting to 23 g.p.l. But the rate of change is only between 4 and 5 g.p.l.p.h. This low rate of change is due to the fact that salt water does not penetrate into those reaches of the Tees in which the duration of the flood-tide has been reduced to 1 to 2 hr." This shows very clearly the necessity of considering the duration of the tides in any discussion of the rate of salinity change.

Apart from tidal changes, there are also seasonal ones caused by rain and evaporation. When much fresh water is flowing down the river, not only will the area of brackish water be more restricted, but the low tide salinity at any point will be abnormally low. In the Berg River in South Africa saline water has been reported over thirty miles from the mouth during the dry season, but after the rains the water at the mouth at low tide is said to be fresh enough to drink. In monsoon climates many estuaries are suddenly flooded by almost fresh water, and this sudden and drastic change kills many of the estuarine inhabitants. Similar drastic changes have already been noted in blind estuaries when the sudden bursting of the bar liberates the accumulated waters of low salinity and allows the sea to sweep in.

Reid (1932) has also shown that the rate of change of salinity in muds and sands is much slower than in open water. He notes that the rate is increased by the strength of the overflowing current and suggests that the slope of the bottom may be important in some way. His work on small streams running into Witsand Bay indicates that the rate of increase is high. It would be interesting to know whether these results are valid for estuarine sand- and mud-banks.

The Effects of Salinity Changes on the Estuarine Populations.—The effects of salinity changes on the other factors of the physical environment are dealt with under the relevant headings, so that we may concentrate here on the direct effects of dissolved salts on the animal population.

Since estuarine waters are constantly varying in salinity, the animals that live there are continually subject to osmotic changes. Thus an animal having wide distribution up and down an estuary must have an efficient osmoregulatory mechanism. While it is beyond the scope of this paper to discuss osmoregulatory mechanisms in detail, the subject is of such importance in estuarine research that brief mention must be made of certain

points. A comprehensive account is given by Krogh (1939), and a discussion of osmoregulation in relation to salt-marsh conditions will be found in Nicol (1935) and Howes (1939).

Animals which tolerate wide ranges of salinity are termed *euryhaline* while those with a limited tolerance are termed *stenohaline*, but these terms have no fixed values, and animals show all grades of salinity tolerance. The majority of marine animals are stenohaline, but it would appear that the concentration of salts in sea-water is higher than is essential for the normal carrying out of the vital functions, so that they will tolerate passively a limited and slow reduction of the external medium with which their body fluids remain isotonic. For example, *Asterias rubens*, whose body fluids are normally isotonic with sea-water of 35 per thousand salinity, is also quite healthy and active in Kiel Bay where its body fluids are isotonic with the brackish water of 14 to 17 per thousand salinity. Possibly it is this passive tolerance to limited dilution of sea-water which allows many typically marine animals to penetrate into the mouths of estuaries where the salinity does not fall below 25 per thousand.

Typical estuarine animals can live in salinities which are much lower than 25 per thousand and in areas where the rate of change of salinity is high. Thus Wells and Ledingham (1940) have shown that salinity changes more rapid than 15 g.p.l.p.h. have no serious effects on *Arenicola marina* or *Nereis diversicolor*, and it will be remembered that this value is the most severe rate of change that Bassindale found in the Severn. Animals which are restricted to estuaries are all euryhaline. Like the stenohaline marine animals, they appear to tolerate passively the first slight reductions of salinity, which incidentally cause swelling and presumably some increase in internal hydrostatic pressure. As the osmotic inflow continues it appears to act as a stimulus, causing a decrease in the permeability of the integuments which slows down the inflow. In certain cases this is followed by the active excretion of hypotonic fluids and even an active absorption of inorganic ions. But this has not been proved in all cases. Whatever mechanism is employed, an osmotic balance is reached, with the internal osmotic pressure lower than the initial value in sea-water but still higher than that of the external medium.

As might be expected, euryhaline estuarine forms have a wide distribution along the length of an estuary, but they are particularly important in the middle reaches where the salinity conditions are most severe where there is an absence of competition from marine forms. It must be noted, however, that the most severe salinity conditions are in open water at the low-tide level, as it has previously been shown that the salinities near the high-tide mark and below the surface of the sand are more stable. This may allow high-tide and burrowing forms, with slightly less efficient osmoregulatory

mechanisms, to have a wider distribution than would be at first apparent. A full discussion of the distribution of estuarine animals in relation to salinity and other physical factors is deferred to the end of this paper.

Freshwater animals are homoiosmotic, *i.e.* they maintain their body fluids at a constant osmotic pressure which is much higher than that of the external fresh water. Many of them appear to secrete a voluminous hypotonic urine and to absorb inorganic ions even from extreme dilutions. It is surprising that so few of them are successful colonisers of estuaries and that the few that do occur are limited to the lowest salinities of less than 5 or 8 per thousand. One suggested reason, as yet unproven, is that the osmotic inflow has become essential to the animal and that under saline conditions this inflow is not sufficiently rapid. Whatever the reason, there are few estuarine animals of freshwater origin and these are restricted to the faintly brackish waters at the head of the estuary.

Very little work has been done on the salinity tolerance of animals living in estuaries more saline than the sea. Even the upper salinity limit of stenohaline marine animals is unknown. Preliminary observations in South Africa indicate that they are absent where the salinity is over 40 per thousand, and that bodies of water with a salinity between 40 and 60 per thousand contain a limited selection of the animals found in normal dilute estuaries where the salinity is between 5 and 20 per thousand. No special hypersaline fauna has been found, and *Artemia* has not been found in estuaries of any sort. If, on further analysis, these observations prove correct, it means that an animal which has evolved an efficient osmoregulatory mechanism is largely independent of increases or decreases in salinity above or below the sea-water value and may be found in all sorts of estuaries. One or two specific examples may be quoted from the South African fauna. *Littorina knysnaensis* is a small periwinkle found on rocky shores in the spray zone and occasionally in salt-encrusted pools at the same level. But it also penetrates into the upper reaches of the Knysna estuary where the salinity falls to 1·4 per thousand at low tide. *Callianassa kraussi* is a burrowing prawn whose habits appear to be identical with those of *C. californiensis* described by MacGintie (1935). *C. kraussi* appears to be present in estuaries all round South Africa and has a known salinity range from 1·25 to 59·5 per thousand. It should be emphasised that this burrowing prawn keeps a continual stream of water moving in and out of its burrow whenever it is submerged. But a third and even more striking example may be quoted. *Mugil cephalus*, the mullet or "springer," occasionally finds its way up from the sea through a series of narrow channels into Little Princess Vlei on the Cape Flats, where the water is barely brackish enough to taste, and has also been recorded from the uppermost parts of

St. Lucia estuary, where the salinity may remain over 50 per thousand for long periods.

The effect of age on salinity tolerance is unknown, but it is certain that most of the migratory forms found in estuaries breed in the sea, and the sudden enriching of the fauna of blind estuaries, which follows the influx of sea-water when the bar is opened, suggests that here again marine conditions are necessary for the breeding or early development of many benthonic forms. An interesting remark on the breeding of *Gammarus* is made by Bassindale (1942): ". . . evidence is accumulating to show that the zone of breeding specimens is restricted during winter and that the extremes of the range—particularly at the less saline end—are occupied by non-breeding or immature specimens."

The Temperature.—The temperature of normal estuaries is initially determined by the temperatures of the river and the sea, and the proportions of each which form the mixture at different states of the tide. Apart from exceptions to be described later, the sea has a more stable temperature so that extremes of temperature are found at the head of the estuary where there is a greater proportion of river water.

The temperature changes with the state of the tide, the time of the day and the season of the year. Francis-Boeuf (1943) states that in France the rivers are colder than the sea during winter, so that there is an increase in temperature as one proceeds down an estuary, but that no generalisation can be made in regard to summer conditions presumably because the origin and thus the temperature of rivers is so variable. But the origin and thus the temperature of marine currents is equally variable. There is a cold current on the west coast of South Africa and a warm one on the east. On this basis one would expect opposite temperature gradients in estuaries emptying on to the two coasts. But generalisations of this sort are of doubtful value, and the only statement with universal validity is that temperature conditions at the mouth are more stable than those higher up the estuary (see Milne, 1938).

It has been noted above that sea temperatures, though usually stable, do occasionally have violent and drastic fluctuations. These are caused by sudden shifts in ocean currents. Thus changes in the position of the Gulf Stream have been recorded which caused mass mortality of fish off the Atlantic coast of North America. Similar shifts of the Agulhas current off the south coast of South Africa have less startling effects but are well known to local anglers, since the change is not only observable by temperature records but by colour differences as well. Smith (1949) gives an account of the phenomenon. The common report is that after the south-east on-shore wind has been blowing for a few days, very blue water appears close inshore and the temperature drops suddenly. It is surprising that

the on-shore wind should have this effect. Actual records of the temperature changes were obtained during an investigation of the Knysna estuary. On March 2, 1948, the temperature at the mouth dropped from 21·8° C. to 11·5° C. within a single day. By the next day the cold water had moved into the estuary and mixed with the warmer brackish water so that the temperature two miles upstream fell from its normal value of 22° C. to 17·4° C. Similar effects were observed at the experimental oyster hatchery a mile from the mouth during November 1948 when the temperature fell from 22° C. to 16° C. in one day.

Although estuarine temperatures are determined primarily by the sea and the rivers, changes also take place within the estuarine basins. Many of these basins are broad and shallow, and thus very susceptible to the warming effects of the sun and to cooling by evaporation. Francis-Boeuf (1943) gives figures to show that air temperatures are unimportant but that there is definite warming by the sun, so that the estuarine temperatures are higher and more variable than the sea. This agrees with observations in South African estuaries.

In the previous section it was noted that the salinity within the sand or mud substratum is more stable than in open water, and it is interesting to know whether temperature variations are similar. MacGintie (1935) states that ten years' records of the "marine" estuary of Elkhorn Slough in California show a variation of open water temperatures between 11° C. and 23° C. and only 12° C. to 19° C. for mud; also that on the same day the surface temperature rose to 23° C., while six inches below the surface of the mud the temperature was only 15° C. An even more interesting observation was that, due to evaporation, exposed mud is cooler than mud under a few inches of water. Nicol (1935) gives rather a different picture for conditions in salt-marsh pools in Scotland. "The temperature in mud varies little from that of the overlying water but may show a lag of a degree or two with rapidly rising or falling temperatures. When, however, the pools are dry, then the temperature of the mud is very often very high at the surface and progressively lower at greater depths." It may be noted that neither of these writers are dealing with normal estuaries and that the different results may be related to the type of substratum and the rate of evaporation. Further research is required.

The Effect of Temperature on the Estuarine Population.—It is well known that the bulk of estuarine animals are derived from the sea. Stephenson and his colleagues have shown that the intertidal fauna of the South African coast is distributed in relation to ocean currents and sea temperatures. While it is not suggested that the estuarine faunas are necessarily intertidal in origin or that their distribution will be found to coincide exactly with the temperature limits of intertidal faunas, yet the work done up to the present

indicates that estuarine faunas also change as one progresses from the temperate waters of the Cape to the subtropical waters of Natal. It is also reasonable to suppose that the freshwater element of estuarine faunas behaves in the same way, but as yet little is known of the ecology of South African rivers.

Not only the species which compose estuarine faunas but also the numbers of species are reported to be related to temperature and latitude, and Nicol (1935) draws attention to the great numbers of species in tropical estuaries as compared with the relatively small numbers in British ones. While the general truth of this is not disputed, the poverty or richness of estuaries depends on so many other factors that the individual effect of temperature may be completely masked.

The effect of extremes of temperature on estuarine populations have been dealt with by a number of authors. Thus Nicol (1935) reports that a variation between 32·5° C. in summer and surface ice in winter had little effect on the fauna of a series of salt-marsh pools in Scotland, and one is left with the impression that this brackish-water fauna is particularly hardy. Bassindale (1943 *a*) also reports that severe winter conditions had little effect on the Severn fauna though seasonal changes in the distribution of amphipods were noted. Hedgpeth (1947) mentions that the fish population of the Laguna Madre of Texas may be exterminated by freezing, but remarks that recovery is rapid. Pratt (1940) reports that ice in the St. Lawrence causes erosion of the estuarine banks and produces a bare zone at about mid-tide level. However, these are all isolated remarks gleaned from papers concerned with other subjects, and a full account of the effect of temperature extremes and the rate of change of temperature is needed.

The relation between seasonal changes in the temperature of estuarine waters and the migration of animals to and from the sea is not completely understood. The movements into an estuary appear to be related to feeding and the return to the sea to spawning, so that the juveniles and adults which appear in the estuary in the spring return to the sea in the autumn of the same or subsequent years.

Many fishes and decapod crustacea take part in such migrations, and evidence is accumulating that the movements are related to both temperature and salinity in that higher temperatures may increase the salinity tolerance. Thus Broekhuysen (1935) has shown that the distribution of the crab *Carcinus maenas* depends on a combination of the two factors and that the salinity tolerance of the developing eggs is increased if the temperature is raised. Broekema (1941) obtained similar results with the shrimp *Crangon crangon*. She says of the seasonal movements: "During winter the animals can be found in the coastal regions of the North Sea and in a

small part of the adjoining shallows; that is to say, in an area of relatively high salinity. During the spring a general migration takes place towards the brackish waters, where the animals remain in great numbers throughout the summer months. Towards autumn the animals again retire to the more saline regions of the total area of distribution." She then shows that osmotic regulation is more efficient at higher temperature, so that in warmer waters the animals can maintain a greater difference between the internal and external salt concentrations, and says: "This result enables us to explain why extremely low or extremely high salinities can better be endured when temperature is high."

Finally, the biological effects of temperature changes due to shifts in sea currents at the mouths of estuaries must be mentioned. It was noted that this occurs at Knysna. When cold water appears along the coast, many fish take refuge within the warmer waters of the estuary and are gradually driven upstream as the cold water penetrates higher with the flood-tide. On these occasions many unusual species are taken, while others that have been trapped in cold water are found numbed. What effect these sudden changes have on the normal sedentary and planktonic population is unknown.

Nutrient Salts.—Relatively little work seems to have been done on the concentration of nutrient salts in estuarine waters. Methods for the estimation of phosphate and nitrates in sea-water are discussed by Harvey (1945), and Cooper (1938) describes the special modifications of the Deniges method of phosphate estimation that is required for estuarine waters. The few estimations that have been made are of interest, because the phosphate values are always higher than for sea-water whereas the nitrate values are lower. Thus MacGintie (1935) reports that the "marine estuary" of Elkhorn Slough of California has four times as much phosphate and silicate as the outside water of Monterey Bay, but that the nitrate values are low. Howes (1939) reports that in an isolated estuarine channel in England, phosphates were very high (1750 mg. per M^3) in the early spring but that nitrates and nitrites were only present as traces.

Some indication why estuaries are relatively rich in phosphate is given by Stephenson (1949): "Estuarine muds in the presence of sea-water sometimes evolve and sometimes absorb phosphate. Generally the surface samples evolve more phosphate than the subsurface samples of mud, and the highest rates of evolution have been obtained with surface samples of grossly polluted muds. Here there is a close correlation between reduction in oxygen concentration of the supernatant sea-water and the rate of phosphate release."

The obvious importance of nutrient salts in estuaries would be as limiting factors in the production of basic plant foods. Whether phosphates and nitrates are as important in estuaries as they are in the sea is not

known; in some cases at least, turbidity must be a more important limiting factor.

Excess Base: Oxygen Concentration: pH.—Since these three factors are intimately related it is convenient to consider them together. A full discussion of their mutual relations in sea-water will be found in Harvey (1945), and special problems in brackish waters in Nicol (1935) and Howes (1939). Since both pH and oxygen concentration are partly dependent on excess base it is convenient to deal with the latter first. Harvey (1945) states: "The (sea) water contains basic radicles in excess of the equivalent strong acid radicles. This excess base is itself equivalent to the bicarbonate, carbonate and borate ions in the water."

The normal concentration of excess base in sea-water is between ·0023 N and ·0026 N, whereas river waters have a much more variable value. It is usually very much lower, so that the concentration of excess base in an estuary increases with the proportion of sea-water in the mixture, *i.e.* it increases with the salinity, and the highest values will be found near the mouth of the estuary at high tide. The importance of excess base is that it takes up the excess carbon dioxide beyond the amount that can be held in free solution in the water, and Howes (1939) has shown that photosynthesis may be inhibited at low carbon dioxide tensions.

The presence of excess basic radicles together with carbonates, bicarbonates and borates, which are all weak acid radicles, gives sea-water a buffer action so that the pH of sea-water is relatively stable between 8·1 and 8·3. River waters are seldom buffered, so that larger variations will be found at the tops of estuaries. The peaty waters of moorland or mountain streams contain a complex mixture of organic acids loosely known as "humic acid." Humus is a negatively charged colloid with a pH averaging 6·5, but on mixing with saline water at the top of the estuary the colloidal humus is coagulated and the pH rises rapidly. Rivers which flow over chalk beds are alkaline with a pH averaging 8·0 to 8·4. These too are buffered by admixture with sea-water.

Variations of pH are usually due to variations in the concentration of free carbon dioxide in solution, a low pH indicating a high concentration of carbon dioxide and *vice versa.* Low pH values will therefore be found in muds with much organic matter where carbon dioxide is being produced by bacterial decomposition; high pH values will be found where plants are abundant, and values up to 9·6 have occasionally been reported. Since photosynthesis takes place only in sunlight, it is not surprising to find that there is a diurnal and seasonal variation not only in carbon dioxide concentration but also in pH and oxygen concentration. Nicol (1935) has demonstrated this in salt-marsh pools in Scotland and found minimum pH values with oxygen below saturation point in the early morning, rising to maximum

pH values and 200 per cent. oxygen saturation in the early afternoon. Broekhuysen (1935) found even greater diurnal variations in a *Zostera* field in Holland. Here the mud had a high organic content, and during the night there was a stench of H_2S and the oxygen concentration was *nil*. By the early afternoon the oxygen concentration had risen to its maximum value of 262 per cent. saturation.

Photosynthesis is only one source of oxygen; the other is the air. Many estuaries are broad and shallow, and can thus absorb a large proportion of the oxygen requirements through the surface layers. This is carried down by turbulence and convection currents, and it is only where these agencies are inadequate that anaerobic conditions are liable to occur. Thus it has been reported that sills at the mouths of some of the Norwegian fjords prevent mixing of the lower layers, so that while the surface layers are well oxygenated and support a rich fauna, the lower layers are practically devoid of oxygen and animal life.

Many writers have drawn attention to the high percentage of organic matter in estuaries both in suspension and deposited as black mud. The bacterial decomposition of this matter absorbs large quantities of oxygen, so that a low oxygen tension may be found in organic muds or in the waters in immediate contact with them. Broekhuysen's figures quoted above indicate that low oxygen tensions, or even an oxygen lack, may exist in water overlying black organic mud during the night and low tide, even though the daylight values are high. Nevertheless it should be emphasised that these oxygen deficiencies are of local occurrence, and that open estuarine waters are usually well supplied with oxygen, even if, as Francis-Boeuf (1943) suggests, they are not so rich in oxygen as the sea.

Three factors have been dealt with in this section. The first is excess base, the biological significance of which is that it holds a reserve of carbon dioxide for photosynthesis which increases the amount of plant food and oxygen available to the animal population. The second is pH, which measures the carbon dioxide tension and thus indicates the balance between photosynthesis on the one hand and bacterial decomposition and respiration by animals and plants on the other. The third is the oxygen concentration itself.

The Plant Population.

Although the flora of individual estuaries differs greatly in quantity and composition, yet the dominant genera are surprisingly widespread. At the mouth of the estuary, where the physical conditions do not differ greatly from the sea, numbers of marine algae will be found. Many of these are local species, but others, particularly *Ulva* and *Enteromorpha*, are euryhaline and penetrate high up the estuary. These have a world-wide distribution.

The attached diatoms are also important; they are insignificant in size and little work has been done on their identification, but they cover vast areas of muddy sand and must be important in the economy of estuaries. Most of the rest of the flora consists of flowering plants many of which have a world-wide distribution. The commonest is *Zostera*, which is usually found at or near the low-tide mark in the more saline areas. The grass-like *Ruppia* is also common at or below low-tide mark, but appears to have a lower salinity range than *Zostera* and to prefer more sheltered areas. Few macroscopic plants live at mid-tide levels, so that there is usually a gap between *Zostera* at the low-tide level and the salt-marsh plants such as *Triglochin*, *Salicornia* and *Juncus* at the top, but occasionally this gap is filled by brack grasses such as *Spartina*. In the tropics the upper levels between neap and spring high-water marks are occupied by mangroves of which *Rhizophora* and *Avicennia* are probably the commonest and have the widest distribution. Mangroves are predominantly tropical but extend into the warm temperate zones of South Africa and Australia. All the genera of plants mentioned here have been recorded from estuaries in England, North America, South Africa and Australia, which indicates how widespread these estuarine plants really are.

The Relation between Plants and Animals.—Plants are important in many ways. Their most obvious rôle is as the source of basic food. This is discussed later under the heading of bionomics. The importance of plants in regard to the concentration of oxygen and carbon dioxide has already been mentioned, but we may add one interesting quotation from Nicol (1935) in regard to the relative efficiency of different plants as oxygen suppliers. She says: ". . . algae as well as diatoms possess the power of saturating water with oxygen to a much greater degree than the higher plants." It would be interesting to know whether this applies to *Zostera*, which was apparently absent from the series of salt-marsh pools on which she was working.

Another important rôle of the larger plants is that they supply a hard substratum raised above the muddy bottom of estuaries and thus allow animals which are normally restricted to rocks to penetrate into those estuaries where large plants occur. The importance of mangroves in this respect is discussed by Fischer (1940). In Australia mangroves carry a fauna of oysters (*Ostrea commercialis* = *O. cuculata*), gastropods such as *Melaraphe*, *Littorina scabra* and *Cerithidea decollata*, and the barnacle *Balanus trigonus*. These and the other animals usually found in mangroves do not constitute a specific mangrove fauna as suggested by Ekman (1935), but are also found on the piles of bridges and other suitable hard substrata, and some of them also extend on to the rocks of the open coast. Fischer's observations have been confirmed in the subtropical estuaries of Natal.

Here also it has been noticed that tough grasses such as *Puccinella* sp. provide a firm substratum for barnacles (*Balanus amphitrite*) and gastropods (*Littorina scabra* and *L. knysnaensis*) which are otherwise restricted to rocks. *Zostera* too provides support for smaller forms including minute gastropods, *e.g. Rissoa* spp., compound ascidians, Polyzoa, Idoteid isopods and even anemones (*Pseudactinia flagellifera*).

Possibly an even more important point is that plants provide shelter. Not only do thick growths of plants reduce the eroding action of the currents and provide shade from the sun when the animals are exposed at low tide, they also provide shelter and harbourage from enemies. Spooner (1947) has drawn attention to the importance of shelter as a limiting factor in the distribution of amphipods in estuaries and remarks that any available cover is made use of, from decaying rubbish to growing weeds. Again, Fischer (1940) shows that mangrove roots provide ideal retreats for the many crabs and mud-skippers that live there. In South African estuaries we have noticed that the epifauna of an open sand- or mud-flat is very poor, but wherever there is an isolated rock, a piece of garbage or a stand of plants such as *Salicornia*, *Puccinella* or, above all, *Zostera* into which the animals may retreat as the tide falls, there we will find a rich fauna of small animals. But the importance of shelter is not restricted to the period of the ebb-tide. Even at high tide, or in those areas where tidal changes are insignificant, a net dragged over a submerged mud-bank will catch far less than a similar drag through *Ruppia* or *Zostera*.

It has been mentioned that plants reduce erosion by currents. This effect may be seen in most estuaries, and Hartley and Spooner (1938) mention the formation of "salting cliffs" in the Tamar. Certain species of *Salicornia*, whose optimum level is between high tide of springs and high tide of neaps, not only stabilise the existing mud but even reduce the current to a sufficient extent to allow the deposition of more mud in its vicinity. "At the same time erosion of edges produces an increasingly abrupt transition line or salting cliff. In the upper reaches of the estuary the top of the salting cliff approximately coincides with the level of ordinary tides." It is surprising how well these observations made in England are duplicated in the Berg River and Knysna estuaries of South Africa.

The Animal Population.

Origin.—The brackish waters of estuaries support a fauna which is derived mainly from the sea, with the addition of a few salt-tolerant freshwater forms and a number of birds. It is usually assumed that the marine animals are necessarily intertidal forms which, being already adapted to the changes of salinity in tidal pools, find no great difficulty in extending their

range into estuaries. While this appears to be generally true for European shores and estuaries where wave action is slight, the hypothesis must be accepted with reserve in South Africa where the majority of the species found on the wave-battered coasts are different from those found in the muddy estuaries. At this early stage in the survey we can only say that common species from the upper zones on the shore such as the crab *Cyclograpsus punctatus*, the isopods *Deto echinata* and *Ligia* spp., the barnacle *Tetraclita serrata* and molluscs such as *Littorina knysnaensis*, *Oxystele variegata*, *Thais dubia*, *Siphonaria capensis* and *S. aspera*, do extend well up some estuaries and maintain their usual level on the shore. But the many species which occur on the lower levels of the open rocky coasts only penetrate into the mouths of estuaries if at all, and higher up the estuaries they are replaced by new groups of animals. Our surveys have not progressed far enough to say to which marine group these estuarine forms are most closely related. It is probable that most intertidal animals in South Africa are adapted to strong surf and are thus not suited to quiet, muddy estuaries. We hope during the course of our survey to compare the fauna of Langebaan (one of the few quiet inlets where there is no freshwater inflow) with the faunas of the open coast and of the nearby Berg River estuary and the shallow waters of Saldanha Bay, and thus throw more light on the origin of estuarine faunas in general.

The Components of an Estuarine Fauna.—It has been mentioned that estuarine faunas are derived from the sea and the fresh water. The freshwater species form a compact group limited to the head of the estuary. But those of marine origin are by no means uniform in distribution. Many of the strong swimmers, including fishes, the larger Crustacea and Cephalopods, are migratory and may enter the estuaries as juveniles and depart as adults; others enter the estuaries at certain seasons to feed, and leave after a few months; others again merely use the estuaries as highways on spawning migrations from the seas to the rivers or *vice versa*; still others are merely casual visitors forced in by unfavourable conditions elsewhere. But the benthonic animals are more stable. Many of these are restricted to the mouth of the estuary where conditions are not very different from the sea; others which populate the middle reaches of the estuary are truly at home there; a few of these are restricted to estuaries but the majority may also be found in the sea.

On the basis of the above distribution and not inquiring for the moment as to its reasons, we may make a few broad divisions of estuarine faunas into faunistic groups or components. These are:

A. *The freshwater component* restricted to waters of low salinity.

B. *The stenohaline marine component* at the mouth of the estuary.

C. *The euryhaline marine component* extending from the sea over the middle reaches of the estuary wherever conditions are suitable.

D. *The estuarine component* comprising the few species which are restricted to estuaries.

E. *The migratory component* which spend only part of their lives in estuaries.

These "components" agree with the faunistic groupings of Percival (1929) as regards benthonic forms, and with those of Hartley (1947) as regards migratory forms. But they are not quite the same as the groupings adopted by Spooner and Moore (1940). These workers were not concerned with the freshwater component or the migratory component, but divided the rest of the fauna into three groups: (A) Essentially Marine (corresponding roughly with the stenohaline marine component mentioned here); (B) Estuarine but occasionally in marine habitats; and (C) Predominantly Estuarine. It is felt that the distinction between groups (B) and (C) is not clear. On the other hand, the small group of animals which are entirely restricted to brackish water should not be included among the euryhaline marine group as is done by Nicol (1936), who divides the bottom fauna into freshwater, marine and brack-water components.

The Distribution of Animals and Plants in Estuaries.

The preceding pages contain a brief review of the physical environment and the origin of the plant and animal population. The animals have further been divided into components as far as this is convenient. It remains to be seen whether there is any logical basis for dividing the estuary into biotic zones. Many workers have made such divisions, but there has been little attempt to relate them to more than a single factor such as salinity, substratum or tidal level. Yet every field worker knows that if one factor such as salinity is right for a particular species, it will not occur in the area unless the other factors such as tidal level and grade of soil are also suitable. The environment must be considered as a whole, and the departure of any factor beyond the range of tolerance will act as a limit to distribution. This is embodied in Liebig's "law of the minimum" and may be expressed graphically thus:

If a burrowing animal which cannot tolerate salinities much below that of the sea also requires a particular grade of sandy mud and a limited amount of exposure such as that between mid-tide and low-tide marks, its distribution will be limited to those areas where these three factors (and possibly others) are all satisfied. The limiting factor to its penetration upstream A would be salinity, the limiting factor at higher B or lower levels C would be exposure, and the limiting factor downstream D would be the absence of suitable

soil. This simplified example is illustrated in fig. 1, but in nature many other factors such as temperature, suitable food, strength of currents, wave action, and oxygen concentration would all play their part in limiting the area colonised. Moreover, recent researches both on South African shores and estuaries indicate that where most of the factors are optimum an animal's tolerance of a few factors may be extended. The tubicolous Polychaet *Gunnarea capensis* is a good example. On the south-eastern coasts the temperature is optimum, and wherever there is sufficient sand and the oceanic swells break off-shore, *Gunnarea* colonises large areas of the

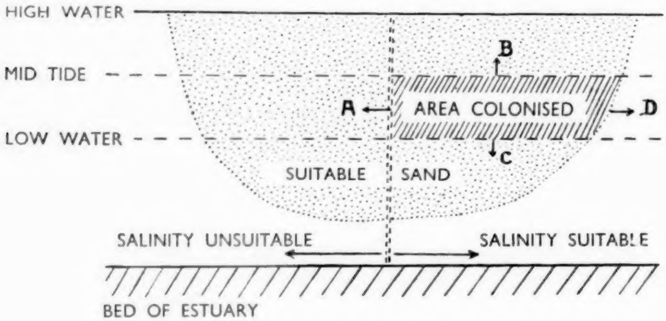

DIAGRAM TO ILLUSTRATE
LIMITING FACTORS IN AN ESTUARY

Fig. 1.

shore from mean sea-level to low-tide mark, *i.e.* from the mid-balanoid zone down to the sub-littoral fringe. This broad vertical distribution continues all the way round the Cape Peninsula and up the west coast as far as St. Helena Bay. Farther north the temperatures are too low, and although the whole coast is very sandy, *Gunnarea* gradually becomes restricted to sheltered bays, and its vertical range on more exposed points tapers to a few inches at low tide of neaps. This suggestion that the optimum of one factor may modify the tolerance of an animal for other factors is very important ecologically. The work of Broekema (1941), quoted earlier, shows the relation between salinity and temperature, but much more experimental evidence on the relation between the distribution, the variations of the physical factors of the environment and the tolerance of an animal to these variations is required before the "law of the minimum" can be restated in a more exact form. The point that is emphasised here is that the distribution of animals in estuaries cannot be based on any single factor of the environment.

Since estuarine animals are not apparently affected by minor changes of salinity, the broad horizontal divisions of the fauna may be related to the major salinity changes in the estuary. Where the changes in the other factors cut across the salinity changes, the distribution of the biota is difficult to follow; fortunately, however, many of the other factors vary in the same way as the salinity, and broad changes of the biota may be observed along the length of the estuary.

A few of the faunistic divisions based on salinity only may be discussed here. One of the earliest is that of Redeke (1922 and 1924).

		Cl. (g./l.)	S. °/₀₀
Fresh water		0·0– 0·1	0·0– 0·2
Brackish water	Oligohaline	0·1– 1·0	0·2– 1·9
	Mesohaline	1·0–10·0	1·9–18·6
	Polyhaline	10·0–17·0	18·6–31·8
Sea-water		17·0–	31·8–

Nicol (1935) criticises these divisions saying: "When an attempt is made to apply it to small bodies of water such as salt-marsh pools it breaks down completely." Work in South Africa indicates that here, too, these salinity ranges do not correspond with major changes of the estuarine faunas.

Percival (1929), after dealing with the components of the population of the Tamar estuary and describing the penetration of the different systematic groups, gives a diagram of distribution in relation to salinity. From this it would seem that most of the marine species disappear when the salinity falls below 30 or 25 per thousand, that many estuarine animals occur between salinities of 20 and 8 per thousand, and that the low salinity species disappear where the salinity falls below 0·1 per thousand. This agrees roughly with what we have found in South Africa.

Nicol (1935) after noting that "For many animals the nature of the substratum appears to be at least as important as the salinity in controlling distribution" gives a graph (fig. 7) showing the distribution of marine, brackish, freshwater and euryhaline species in relation to salinity. From this it is evident that there is a big drop in the number of marine species between salinities of 35 and 25 per thousand, that the animals of freshwater origin disappear in salinities above 5 per thousand, and she says that this phenomenon has been shown to occur in Randersfjord by Johansson (1918) and Remane (1934). Unfortunately these papers are not available to the present writer. Nicol further states that the maximum number of brackish-water species occur at a salinity of 25 per thousand, but an examination of her figure 7 shows very little difference in the number of brackish-water species between salinities of 15 and 30 per thousand.

On the basis of the above evidence and from what we have observed in South Africa, it would appear that the maximum changes in estuarine faunas are associated with salinities of 25, 15, 5 and 0·1 per thousand. The stenohaline marine component disappears when the salinity falls from the sea-water value to about 25 per thousand. The euryhaline marine component can tolerate lower salinities, but is much reduced below salinities of 15 per thousand and disappears at about 5 per thousand. The estuarine component is widely distributed between salinities of 25 and 5 per thousand but can tolerate a wider range than this. The freshwater component is found between salinities of 0·1 and about 5 per thousand. The migratory component can move up and down the estuary to escape severe salinity conditions and are thus of no value in assessing the faunistic divisions of an estuary.

At this stage of our knowledge there is no point in generalising about the faunistic divisions of estuaries which are blind for most of the year or those with reversed salinity gradients. The only profitable course is to outline the divisions in a typical estuary with an open mouth, a normal inflow from a river, and a reasonable tidal range. This may be used later as a background against which the conditions in more specialised estuaries can be compared.

In such a typical estuary, salinities below 5 per thousand are restricted to the head of the estuary, and salinities between 5 and 15 per thousand occur in the slow channels of the upper reaches. Salinities between 15 and 25 per thousand occur in the middle reaches, and salinities above 25 per thousand are restricted to the seaward entrance. It is not suggested that these limits are definite; they merely indicate the progressive changes along the length of an estuary. Variations in salinity will occur with the state of the tide, from neaps to springs and from the dry to the rainy season.

So much for faunistic divisions based on differences of salinity. It is now necessary to consider the effect of the other factors. Wave action is restricted to the mouth of an estuary and thus has no effect on the distribution of animals upstream. But variations of current strength deserve more consideration. It has been shown that currents have important direct effects on animals and that they determine the distribution of sediments and the degree of turbidity in different parts of an estuary, and that, in the absence of currents, soft muds deficient in oxygen are deposited. So all these important factors have a related distribution. Apart from the effect of local constrictions where currents are strong, most estuaries gradually broaden towards the sea, but the mouth itself is often constricted by sandbanks. River currents lose their strength at the head of an estuary and the tidal currents have spent their force, so that the upper reaches are quiet and slow-flowing. Lower down, the currents in the main channels increase in strength although the tides flow slowly over the upper banks and into the

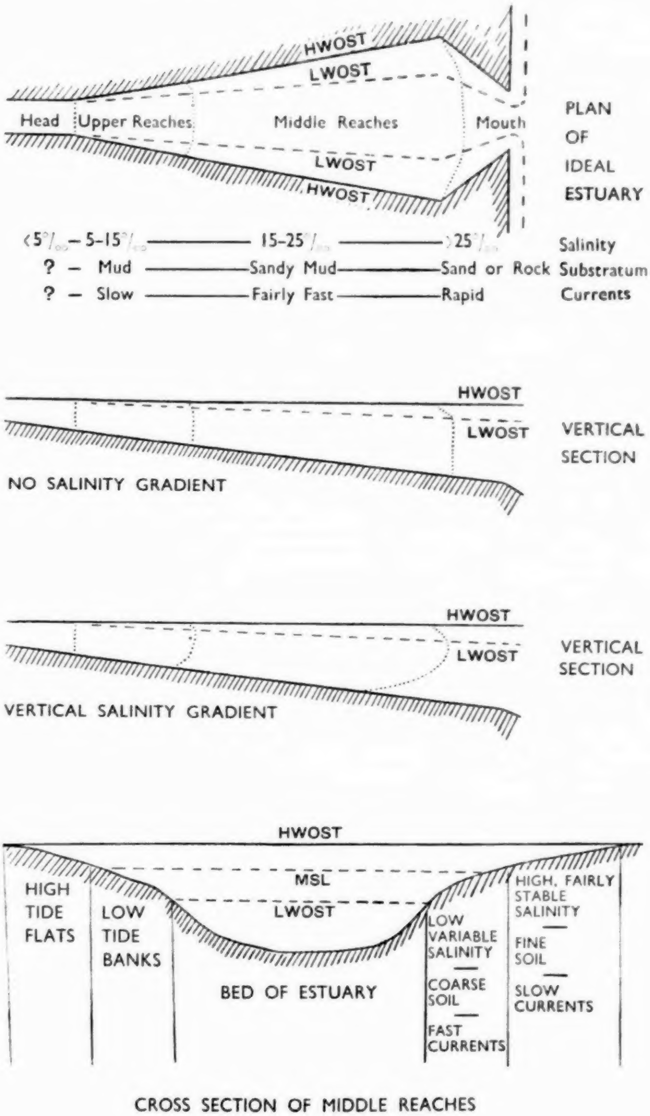
HWOST
LWOST
Head
Upper Reaches
Middle Reaches
Mouth
LWOST
HWOST
PLAN OF IDEAL ESTUARY
<5‰ – 5-15‰ — 15-25‰ — >25‰ Salinity
? – Mud — Sandy Mud — Sand or Rock Substratum
? – Slow — Fairly Fast — Rapid Currents
HWOST
LWOST
VERTICAL SECTION
NO SALINITY GRADIENT
HWOST
LWOST
VERTICAL SECTION
VERTICAL SALINITY GRADIENT
HWOST
MSL
LWOST
HIGH TIDE FLATS
LOW TIDE BANKS
BED OF ESTUARY
LOW VARIABLE SALINITY
COARSE SOIL
FAST CURRENTS
HIGH, FAIRLY STABLE SALINITY
FINE SOIL
SLOW CURRENTS
CROSS SECTION OF MIDDLE REACHES

Fig. 2.

backwaters. But the channels at the mouth must not only serve as an exit for the river waters, they must also carry all the water which moves in or sweeps out with the tide. These are the strongest currents.

With this background we can now consider the physical conditions in the different sections of an estuary, remembering that this is an idealised picture, that the changes in the various factors are not always co-extensive, and that local peculiarities will be found in any individual estuary.

At the *head of the estuary* the main change from normal river conditions is that there is a slight amount of salt in the water at high tide of springs, but at low tide and during neaps this is largely swept down and the fauna consists of those freshwater forms which can tolerate a slight amount of salt.

In the *upper reaches of the estuary* saline water is always present. The strength of the river current is much reduced by the inflowing of the tide and the broadening of the basin. But the amount of water which enters with the rising tide is not sufficient to create strong currents on the ebb. Under conditions of increased salinity and decreasing currents the fine silt carried down the river is deposited as mud. This region (which is separated from the head of the estuary with some doubt) has a very poor fauna of mud-loving estuarine forms. Most of them live on the surface of the mud, for the deeper layers commonly lack oxygen. The upper tidal banks form extensive salt marshes separated by "salting cliffs" from the winding channels.

The *middle reaches of the estuary* have a salinity range of roughly 15 to 25 per thousand depending on distance from the sea and tidal level. The substratum consists of sandy mud, varying in texture with the tidal level, current strength and distance from the sea. There are finer muds at the top of the shore and coarser mixtures of sandy mud at the low-tide mark. The population consists of the estuarine component and euryhaline marine component, and the majority are burrowing forms. Rich beds of *Zostera* are common at or near the low-tide level depending on the turbidity. *Salicornia*, *Spartina* and other salt-marsh plants are common at the upper levels, and in the tropics mangroves flourish.

At the *mouth of the estuary* the salinity seldom falls below 25 per thousand. There is a certain amount of wave action, and this together with the strong currents prevents the settling of fine silt so that the substratum varies from bare, clean rocks and pebbles to clean, coarse sands. Turbidity is relatively low. The area is colonised by the stenohaline marine component; quite a number of sea-weeds are found extending often below the tide marks. Burrowing animals are scarcer than in the middle reaches because the clean sands contain little detritus and the strong currents do not favour the construction of burrows. Rock-loving forms which prefer a small amount of wave action and can stand a limited reduction of salinity (*e.g.* Oysters) are

common. If a vertical salinity gradient exists, these marine animals can extend farther up the bed of the estuary as well as near the high-tide mark.

These faunistic divisions have been referred to as the head, the upper reaches, the middle reaches and the mouth for lack of better terms. They represent four successive zones along the length of the estuary and may not really correspond with the parts named. Depending on local conditions, any one zone may extend over a longer or shorter stretch. It is hoped, however, that these divisions will provide a useful guide for the more accurate description of a very complex distribution and serve as an introduction to further work on the estuaries of South Africa.

The Bionomics of Estuaries.

The food chains in the sea have been studied by many workers, and since many of the same species also inhabit estuaries we have a good foundation to work on. But there is a major difference between the two environments, for the basic food in the sea is phytoplankton, but this is scarce in estuaries, and attached plants are the basis of life. Some few herbivores feed directly on living plants. Thus Ghazzawi (1935) has shown that attached diatoms are important in the diet of Mugilid fishes, which are so common and so important in many warm-water estuaries. Living *Enteromorpha* is eaten by a variety of gastropods and fishes, and the Sirenia are said to browse on *Zostera*. But the majority of the estuarine "herbivores" feed on the breakdown products of these plants in the form of detritus. *Zostera* is probably the most important source of detritus in most estuaries, but *Ruppia*, *Enteromorpha* and a host of other plants also contribute to the fine mass of decaying vegetation, bacteria and microscopic animals which accumulates on the bottom. The whole question is discussed by MacGintie (1935), who shows that diatoms are relatively unimportant in the diet of many benthonic "herbivores" such as clams, *Upogebia*, *Callianassa* and *Urechis*, and that their main food is this detritus in which the bacteria may be an important constituent. His feeding experiments have shown that *Urechis* grows more rapidly when fed on a pure bacterial suspension.

Detritus drifts along in the estuarine currents, to be deposited on the bottom in the quieter areas and eventually covered with further layers of mud or sand. Animals feed on it at every stage of its journey, and examples of the various feeding methods are given by Yonge (1949). While still suspended in the water, it is filtered out by fan worms (e.g. *Sabella*), the burrowing prawn (*Upogebia*), and many bivalves such as *Solen*, *Cardium* and *Mya*. Once it comes to rest on the bottom it is devoured by shrimps, prawns, mysids, *Corophium* and other amphipods, as they crawl over the surface, or it is sucked down by the searching siphons of bivalves like

Macoma and *Scrobicularia*, or adheres to the sticky tentacles of Terebellid Polychaets and Holothurians. When buried, it becomes available to the "mud-swallowers" like *Arenicola*, or "sand-sifters" like *Callianassa*. These detritus feeders are the foundation members of longer or shorter food chains. According to size and habitat, they are eagerly devoured by a host of small predators like Nemertines, whelks, crabs, starfishes and fish. All of these, as well as the larger detritus feeders themselves, form the food of the larger predaceous fishes and the birds. The majority of these are migratory, and Hartley (1947) has summed up the matter by saying: "The essential organisation of animal life in an estuary is that of a resident population providing food for a number of migratory predators."

The links in the food chain vary with the type of estuary and the season. This is best illustrated from our notes on three South African estuaries. The Klein River estuary is cut off from the sea for most of the year, and the important plant food is *Ruppia*. Detritus feeders include abundant amphipods, mysids, a few shrimps and large numbers of the burrowing sand prawn *Callianassa*. The common fishes are *Rhabdosargus globiceps*, *Lithognathus lithognathus* and *Mugil capito*. The Mugils feed on attached diatoms and probably also on filamentous algae and detritus, but *Rhabdosargus* and *Lithognathus* prey on the detritus-feeding Crustacea.

In the warmer Knysna estuary, which is permanently open to the sea, the basic plant food is *Zostera*. Detritus feeders include amphipods, shrimps, and large numbers of the burrowing mud-prawn *Upogebia*. The common fishes are *Mugil* spp., *Rhabdosargus tricuspidens*, *Lithognathus lithognathus* and *Johnius hololepidota*. The Mugils are again herbivorous, and the other three are carnivorous and feed on the Crustacea. Large specimens of *Johnius hololepidota* as well as *Lichia amia* feed on the Mugils.

In the subtropical Richards Bay estuary in Natal, *Zostera* is again the most important plant, detritus feeders include mysids, shrimps and Penaeid prawns, and the common fishes are *Mugil* spp., *Rhabdosargus* spp., *Johnius* spp., *Pomadasys* spp. and many others. The Mugils occupy the same niche as before, but it is interesting that in this case most of the larger predaceous fishes seem to feed on the Penaeid prawns and follow them into the estuary in spring and out in the autumn.

In comparison with English estuaries it is noteworthy that bivalve molluscs are relatively scarce, while various species of prawns are abundant. In both, mysids are important.

These few notes are given to illustrate the following points:

(1) *Zostera* is the most important plant food in the middle reaches of open estuaries, but may be replaced by brack grasses in closed estuaries and the higher reaches.

(2) Detritus formed from *Zostera* or other plants feeds a great variety of animals of which Crustacea and bivalve molluscs are the most important. Amphipods and mysids are always present in large numbers, but the larger detritus feeders differ from place to place. Detritus feeders are usually permanent residents, but the tropical penaeid prawns are migratory.

(3) Much work remains to be done, but, as far as is known, all the large carnivorous fishes are migratory. They spawn in the sea and use the estuaries as nurseries or as feeding grounds.

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A FOSSIL LAMELLIBRANCH FROM THE MIDDLE ECCA BEDS IN THE KLIP-RIVER COALFIELD NEAR DUNDEE, NATAL.

By Michael H. P. Rilett.

(With Plate XII.)

(*Published by permission of the Honourable the Minister of Mines.*)

(Read March 15, 1950.)

Abstract.

A new species of *Unio* is described and the range in time of this genus has been extended to the Early Permian.

Introduction.

Specimens of a fossil lamellibranch, undoubtedly *Unio*, were obtained during the course of mining operations at the Aletta Iron-Ore Mine. Further but very badly preserved and broken specimens have been found in surface quarries on the neighbouring farm, Stanmore 2412. The iron-ore bed consists of three feet of carbonaceous siderite overlain by six inches of coal, and contains occasional but unidentifiable plant remains. The deposit is lenticular, is clearly lacustrine in origin, and occurs some eighty feet below the main coal zone.

The horizon of these fossils is thus about six hundred feet above the base of the Middle Ecca and about four hundred and fifty feet below the base of the Upper Ecca shales. This genus, whilst known from the Upper Triassic of Europe and North America and from beds of apparently the same age in East Africa, has not, to the author's knowledge, been previously identified in beds of Permian age.

Family UNIONIDAE.

Genus Unio A. J. Retzius, 1788.

Unio alettaensis sp. nov.

Specific Characters.—Shell inequilateral and equivalve, elongate and moderately inflated, length approximately twice the height. Umbones

broad and situated at the anterior third of the length. The umbones are bent slightly towards the anterior margin, and the beaks are separated by some four to five millimetres. Both posterior and anterior margins are slightly convex and make obtuse angles with the dorsal margin. There is a well-defined angle between the posterior margin and the ventral margin, which is symmetrical and slightly convex. Postero-dorsal margin slightly concave. The margins are smooth. Surface bears well-marked growth rugae. Ligament indistinct. Internal characters unknown.

Dimensions.—Holotype length 46 mm., height 24 mm., inflation 16 mm.

Paratypes.—Length from 46 mm. to 60 mm., height from 24 mm. to 40 mm., inflation from 16 mm. to 25 mm.

The largest specimen is crushed and the next largest has the greatest inflation.

Material.—Six specimens. As the smallest is the most perfect it is chosen as holotype, although the umbones are missing from it.

Locality.—Aletta 4350, Dundee District, Natal.

Remarks.—Most of the original shell-matter in the specimens has been replaced by a mixture of siderite, the iron oxides, clay and a small amount of manganese oxide. Except in two specimens where portions of the shell are missing, the external form has been preserved in its entirety. The valves are joined together, and the interior of the shells are filled with a fine-grained sand cemented with siderite. Professor L. C. King, of the University of Natal, kindly allowed me to examine two internal moulds of this species. In the left valve of one of these specimens there is an impression just in front of the umbo which may be a tooth, otherwise there are no signs of dentition. There are well-developed muscle scars just in front of the umbo in both valves.

The shells were slightly damaged by the blasting and rough handling in the mine. Some of the specimens are crushed. Any umbonal sculpture which may have been originally present has been destroyed.

Some twenty years ago a specimen of a lamellibranch was found in the torbanite seam at Wakkerstroom in the Transvaal. It was referred to the late Dr. A. L. du Toit (2) and was tentatively referred by him to the genus *Carbonicola* (*Anthracosia*). This specimen cannot be located, but a further example, from the same locality, was found by Mr. H. N. Visser of the Geological Survey in 1940. This latter was fortunately available for comparison, and although it is badly preserved it differs from the species now described in that the postero-dorsal margin is slightly convex, and the inflation is proportionately much greater. The umbones of the Wakkerstroom specimen are indistinct, so the genus will always remain in doubt. The author is convinced that the species now described cannot be referred to *Carbonicola* as the beaks are fairly widely spaced.

Externally these shells agree closely with the Triassic forms of North America and East Africa. They differ from *U. karrooensis* Cox (1), *U. dumblei* Simpson (3), and *U. emersoni* Troxell (4) by being rather more inflated and less elongate. The shells are smaller than in *U. karrooensis* Cox (1), but are larger than the other forms mentioned. The umbones in the species described are more prominent than in the above forms. In shape *U. alettaensis* agrees most closely with *U. dockumensis* Simpson (3), but differs from this and all the above forms mentioned in that the postero-dorsal margin is concave.

The holotype, MR 12, and the paratypes, MR 13 to MR 17, are preserved in the collection of the Geological Survey in Pretoria.

The author wishes to express his thanks to the management and staff of the Aletta Iron-Ore Mine for presenting him with the specimens and showing him the place of excavation. He also wishes to thank Dr. S. H. Haughton of the Geological Survey who gave him much encouragement and valuable advice.

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DESCRIPTION OF PLATE.

Fig. 1. *Unio allettaensis* sp. nov. Lateral view. Specimen No. MR 12. × $1\frac{1}{8}$.
Fig. 2. *Unio allettaensis* sp. nov. Anterior view. Specimen No. MR 13. × $1\frac{1}{8}$.
Fig. 3. *Unio allettaensis* sp. nov. Lateral view. Specimen No. MR 14. × 2.

Fig. 1.

Fig. 2.

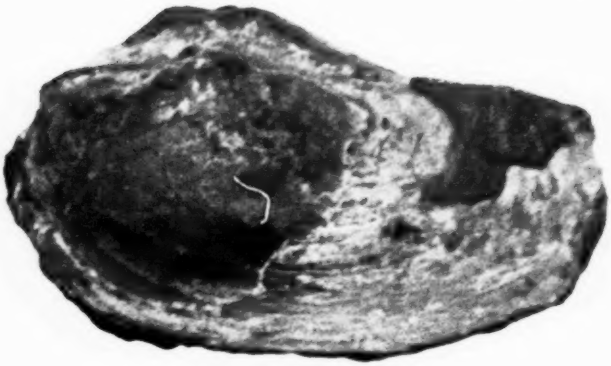

Fig. 3.

M. H. P. Edett. Neill & Co., Ltd.

REVIEW OF TWO BOOKS BY PROFESSOR J. E. HOFMANN.

I. Leibniz's mathematische Studien in Paris, Walter de Gruyter, Berlin, 1948.

II. Die Entwicklungsgeschichte der Leibnizschen Mathematik, Leibniz Verlag, Munich, 1949.

By Dr. C. Y. Pauc, University of Cape Town.

(With three Text-figures.)

(Read March 15, 1950.)

In connection with the tercentenary of Leibniz's birth in 1946, Professor J. E. Hofmann was entrusted, in 1940, by the "Preussische Akademie der Wissenschaften", with the edition of the works of the German mathematician and philosopher. The publications under review are products of the thorough, painstaking activity of a scholar to whom, for at least four years (1940–1944), most of the original sources of information concerning the historical background and origin of the Calculus were available. Long lists of documents are given, with footnotes referring to them, but it is a definite merit of the author that he does not scare the reader by his erudition. On the contrary, he induces in him a feeling of reliability, objectivity; he gives him an opportunity—if he wishes—to form his own opinion on the topics expounded or touched upon, such as the indebtedness of Newton and Leibniz to their predecessors, the influence of Leibniz's correspondence with the Royal Society on his development, the rôle of Leibniz's symbolism and so on.

I and II present the evolution of Leibniz's mathematics during the most creative years of his mathematical life, his stay in Paris (1672–1676) interrupted by two visits to London in 1673 and 1676. II is more detailed than I—on almost every page mathematical quotations are found which are generally either completely worked out or can be by anyone familiar with the Calculus. I may be read as a literary essay with a view to the historical and general scientific background. To derive full profit from II it is

advisable to take a pen or a pencil and to follow, or even to reconstruct, the original proofs. Modern notation is used throughout.

At the beginning we are given an idea of the modest mathematical knowledge of Leibniz when he arrived in Paris, in March 1672, on a political mission. Under the stimulating influence of Huygens he started studying the standard works of that time, especially Pascal. From Pascal's computation of the "moment" $\int_0^{\frac{a\pi}{2}} y ds$ of a quadrant of a circumference $\left(x=a\cos\frac{s}{a},\ y=a\sin\frac{s}{a},\ 0<s<\frac{a\pi}{2}\right)$ with respect to the x-axis, he derived his notion of the "characteristic triangle" of a curve $y=f(x)$ (*i.e.* the triangle whose vertices are (x, y), $(x+dx, y)$, $(x+dx, y+dy)$). Studying the computations with infinitesimals in Pascal's "Lettres", he arrived at the idea of decomposing a segment into small triangles with a common vertex, and devised his "Transmutation Method" (1673), AB denoting the graph of the positive "smooth" function $y=f(x)$, $0<a<x<b$, T $(0, z)$ the point of intersection of the tangent at P (x, y) with the y-axis, Q $(x+dx, y+dy)$, U (x, z), V $(x+dx, z)$, R $(x, 0)$, S $(x+dx, 0)$, F $(a, 0)$, A $(a, f(a))$, G $(b, 0)$, B $(b, f(b))$, H $(a, z(a))$, I $(b, z(b))$; simple geometrical considerations show that

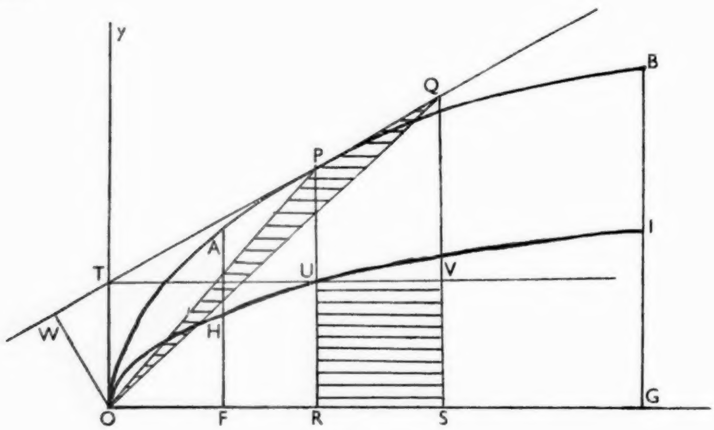

FIG. 1.

Area of the triangle OPQ $=\frac{1}{2}$ area of the rectangle RUVS.

Therefore

Area of the sector OAB $=\frac{1}{2}$ area of the segment FHIG.

Leibniz was thus able to subsume under a general method the isolated "integrations" he had come across so far. For instance, the quadrature problem for the parabolae of higher order

$$\left(\frac{y}{b}\right)^q = \left(\frac{x}{a}\right)^p$$

(p and q positive integers) previously solved by Torricelli, Fermat and Huygens, could be treated on account of the relation

$$z = \left(\frac{q-p}{q}\right)y,$$

a consequence of Torricelli's result,

$$\frac{q\,dy}{y} = \frac{p\,dx}{x}.$$

In the same year, 1673, still using his "Transmutation Method", he produced his arithmetical quadrature of the circle. In the case of the circle $y = \sqrt{2ax - x^2}$ we have the relations

$$\frac{z}{a} = \frac{y}{2a - x} = \frac{x}{y} = z\sqrt{\frac{x}{2a - x}}, \qquad x = \frac{2az^2}{a^2 + z^2}.$$

The circle sector

$$S = \tfrac{1}{2}az - \int_0^z \frac{az^2dz}{a^2 + z^2}.$$

We have here the first example of a rationalizing process * to calculate an integral. Leibniz then follows Mercator's procedure † for $\int \frac{dx}{1+x}$, dividing az^2 by $a^2 + z^2$, expanding in a series and integrating term by term

$$S = \frac{1}{2}az - \frac{z^3}{3a} + \frac{z^5}{5a^3} - \ \cdot \ \cdot \ \cdot$$

For $z = a$, it yields the "Leibniz series",

$$\frac{\pi}{4} = \frac{1}{1} - \frac{1}{3} + \frac{1}{5} - \frac{1}{7} + \ \cdot \ \cdot \ \cdot$$

After such initial successes in setting up a unifying method, having thoroughly studied the special infinitesimal computations available to him,

* In the modern sense of the word it means the transformation of the integral of a non-rational function into the integral of a rational one by means of a substitution.

† Given in his "Logarithmotechnia", London, 1668.

and having acquired manipulative skill in algebraic problems, Leibniz gradually created the suitable symbolism, an "ars inveniendi" (technique of discovery), for problems involving infinitesimals. He replaced the Cavalieri-Fabri notation, "omn y ad x" ("omn" stands for "omnes", all), first by $\int y$—$\int$ representing a long S—and finally by $\int y dx$. He introduced the notation $\frac{dy}{dx}$. Adopting Descartes's distinction between "geometrical" (now "algebraic") and "mechanical" (now "transcendent") problems and functions, he tried to devise algebraicity tests, to typify the problems depending on the quadrature of the circle and of the hyperbola (in modern terminology: involving the trigonometric and logarithmic functions), using rationalizing processes. In the purely algebraic field he established the validity of Cardan's formula for the roots of a cubic equation when there are three real roots (the so-called "irreducible case"). An equation like

$$\sqrt{1+\sqrt{-3}}+\sqrt{1-\sqrt{-3}}=\sqrt{6},$$

which perplexed Wallis, had for Leibniz its present meaning, namely, that $f(x+iy)+f(x-iy)$ for a real function f and real x and y represents a real number. He investigated equations which can be solved by generalized Cardan formulae, and determined all the integer solutions of a system of linear equations with integer coefficients (linear Diophantine problems).

The essential contribution of Leibniz consisted in replacing consciously in the infinitesimal field the old geometrical viewpoint, inherited from the Greeks, by the modern analytic, functional one. Newton, before Leibniz—the manuscript of his "Analysis" was ready in 1669—achieved the same result by means of his power series expansions, initially obtained through the division of polynomials or the extraction of square roots of polynomials (such operations being entirely similar to those used with numbers written in the decimal notation). Newton manipulated power series like polynomials, differentiating and integrating them term by term. We find the same tendency in Gregory, who, originally influenced by Newton, proceeded in the same way with interpolation series. As early as 1670 he was in possession of the formula *

$$f(x_0+n\Delta x)=f(x_0)+\binom{n}{1}\Delta f_0+\binom{n}{2}\Delta^2 f_0+\ \ldots$$

which he assumed to be true for any value of n and which he integrated term by term with respect to n.

Two examples, borrowed from II, of integration processes before the

* The finite differences $\Delta^j f_q$ for *fixed* Δx are defined as follows:

$$\Delta^1 f_1=\Delta f_i=f(x_{i+1})-f(x_i) \quad \text{where} \quad x_i=x_0+i\Delta x, \quad \Delta^{p+1} f_i=\Delta^p f_{i+1}-\Delta^p f_i.$$

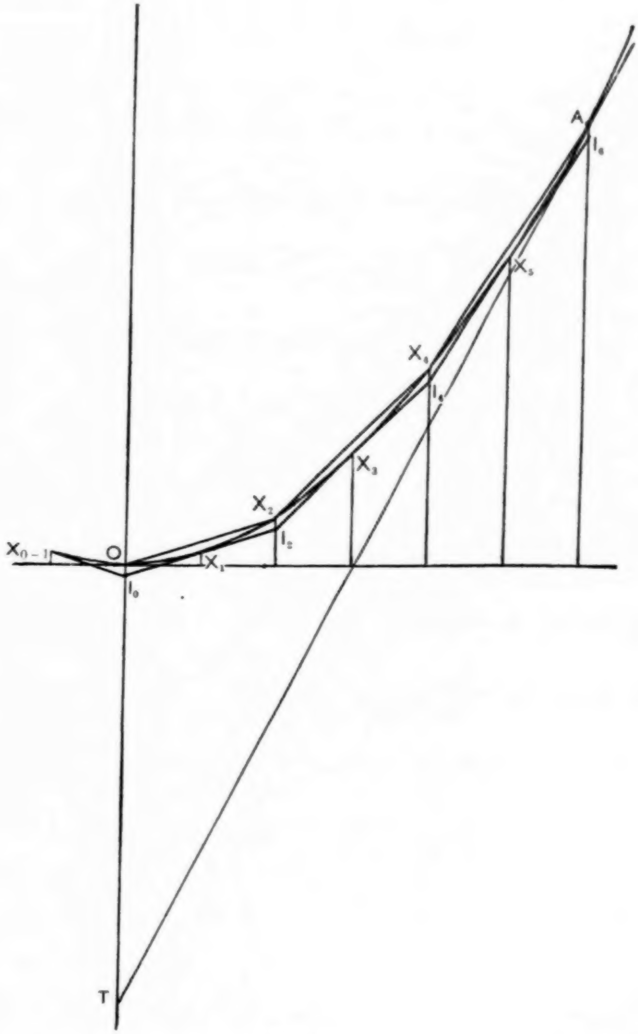

FIG. 2

creation of the Calculus are given here. They may place the reader in the atmosphere of the period immediately preceding the great discovery. The first one is Huygens's rectification of the parabolic segment (1657). The equation of the parabola is $\frac{y}{b}=\left(\frac{x}{a}\right)^2$, s represents the length of the segment from the apex O (0, 0) to the point A (a, b). T is the point of intersection of the tangent to the parabola at A with the y-axis, $t=\mathrm{AT}=\sqrt{a^2+4b^2}$, X_i is the point of the parabola with the abscissa $x_i=i\frac{a}{2n}$ (n a positive integer, i an arbitrary integer), I_i the point of intersection of the tangents at X_{i-1} and X_{i+1}—it has the abscissa x_i. The length s_n of the inscribed polygon $\mathrm{X}_0\mathrm{X}_2 \ldots \mathrm{X}_{2n}$ yields a lower approximation for s. An upper approximation is given by the length S_n of the circumscribed polygon $\mathrm{X}_{-1}\mathrm{I}_0\mathrm{X}_1\mathrm{I}_2\mathrm{X}_3 \ldots \mathrm{X}_{2n-1}\mathrm{T}_{2n}\mathrm{X}_{2n+1}$. Since $\mathrm{X}_{i-1}\mathrm{X}_{i+1}=\mathrm{I}_{i-1}\mathrm{I}_{i+1}$, the difference $S_n-s_n=\mathrm{X}_{-1}\mathrm{I}_0+\mathrm{T}_{2n}\mathrm{X}_{2n+1}$ can be made arbitrarily small for sufficiently large n. This is the kernel of Huygens's existence proof, which is of Euclidean type and rests essentially on special properties of the parabola. As for the expression for s, Huygens compares the length of the chord of the parabola having the end abscissae $x+\Delta x$ and $x-\Delta x$, approximately $\sqrt{1+\frac{4b^2x^2}{a^4}}\,\Delta x$, with the length of the segment on AT having the same end abscissae, which is $\sqrt{1+\frac{4b^2}{x^2}}\,\Delta x$. Introducing the hyperbola $z=\sqrt{a^2+\frac{4b^2x^2}{a^2}}$, he derived by geometric integration,

$$\frac{s}{t}=\frac{\text{area of the hyperbolic segment OCDE}}{\text{area of the rectangle OFDE}}.$$

In communicating his result without proof, Huygens gives s as the height of a rectangle with length $\mathrm{OE}=a$ equivalent to the hyperbolic segment. The quadrature of an hyperbolic segment had been achieved before Huygens by means of the logarithmic function (fig. 3).

The second example mentioned above is Fermat's quadrature of the segment S of the generalized parabola

$$\left(\frac{y}{b}\right)^n=\left(\frac{x}{a}\right)^m \quad \text{for } 0<x<a,$$

where m and n are positive integers prime to each other. t being a number between 0 and 1, to

$$x_k=at^{kn}, \quad k=1, 2, \ldots$$

there corresponds a value of y,

$$y_k=bt^{km}.$$

The parabolic segment S_k from x_k to x_{k-1} contains the rectangle

$$R_k = (x_{k-1} - x_k)y_k = ab(1 - t^n)t^m t^{(k-1)(m+n)}.$$

Hence

$$S > \Sigma R_k = ab\frac{(1 - t^n)t^m}{1 - t^{m+n}}$$

$$= ab\frac{(1 + t + \ . \ . \ . \ + t^{n-1})t^m}{1 + t + \ . \ . \ . \ + t^{m+n-1}}.$$

For $t \rightarrow 1$, the step figure formed by the union of the R_k tends to the segment, therefore

$$S = \frac{abn}{m + n}.$$

In these examples the difference with the Calculus appears clearly. The old method is ingenious and illuminating because it goes deep into the

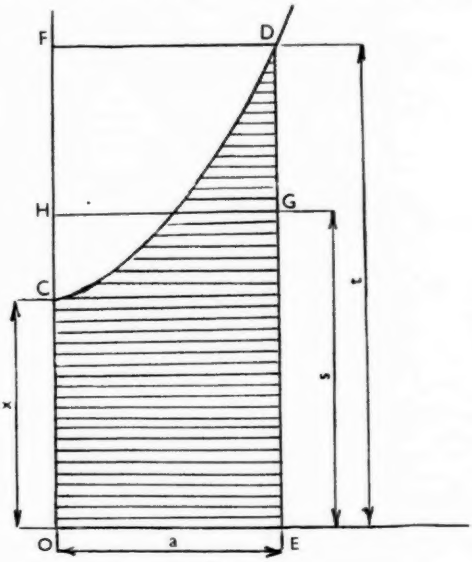

FIG. 3.

special problem, but its application is limited to the problem studied or, at least, the mathematician did not try to abstract the general features. In Huygens's rectification, if we interpret z as

$$a \times \text{slope of the tangent to the curve,}$$

we define the "transmutation" of a rectification problem into a quadrature problem, which is general. The new method is purely algorithmical, its application depends on the analytical structure of the integrand. It teaches us little about the special problem, but leads us quickly to the result without requiring much initiative. "Economy of thought" was to be an essential feature of Leibniz's symbolism. Leibniz's Calculus, according to its inventor, was only part of his "calculus of deductive reasoning", applicable to all kinds of reasoning which would now (he hoped) be reduced to manipulation of formulae according to prescribed rules.

The relations of Leibniz with the leading French and English mathematicians form the texture of I and II. The author has tried to unravel, in complete objectivity, the complex of misunderstandings which brought about the famous controversy regarding the inventor of the Calculus. His final conclusion agrees with the now almost universal opinion, namely, that Leibniz invented his own Calculus later than Newton, and independently. He emphasizes the importance of the Scotsman Gregory, which has been recognized only recently.* Gregory approached the Calculus through interpolation series (1668). Newton's series for finding the area of a zone of a circle was communicated to him in 1670, viz.

$$2RB - \frac{B^3}{8R} - \frac{B^6}{20R^3} - \ . \ . \ .$$

where R denotes the radius of the circle, and B the distance of the chord to the parallel diameter bounding the zone. Being just occupied in elaborating his own ideas finally, Gregory was able to rediscover the method of power series and to set up, in 1671, the so-called "Taylor" expansion in the form

$$y = y_0 + \frac{x}{r} r y_0' + \frac{x^2}{2r^2} r y_0'' + \ . \ . \ .$$

The main source of information is the voluminous correspondence listed at the end of each book. The letters between Leibniz and the Royal Society, especially those with Newton, are carefully analysed. The reading conveys an impression of intense life which reminds one of a dramatic play. It starts with the blunders of Leibniz on the occasion of his first stay in London, due to his exaggerated self-confidence and his ignorance of the achievements of the French and English. It finishes with the second letter of Newton, where Leibniz could feel an insinuation of plagiarism, and the last letter of Collins, the mathematical counsellor of the Royal Society, in charge of the foreign correspondence. Collins had allowed Leibniz, during his second stay in London, to write abstracts of unpublished mathematical

* See Tercentenary Memorial Volume, ed. H. W. Turnbull, London, 1939.

papers of Gregory and Newton without their knowledge. Regretting his action, he cut off the correspondence with Leibniz in spite of the latter's desire to keep in touch with the British mathematicians.

I and II are not intended for specialists, and to a large extent may be read without consulting any of the numerous references. At a few places, however, the quotations are so concise as to make reconstruction difficult without any further knowledge. For instance, in II, p. 19, Newton's expression of the sum s of a finite number of terms of a "musical progression" * is given, viz.

$$s=\frac{a}{b}+\frac{a}{b+d}+\frac{a}{b+2d}+\ .\ .\ .\ +\frac{a}{c-d}+\frac{a}{c}=\frac{a}{\bar{e}}\log_e\frac{n}{m}:\log_e\frac{2\bar{e}+d}{2\bar{e}-d},$$

where $m=b-\frac{1}{2}d$, $n=c+\frac{1}{2}d$, $\bar{e}=$ convenient number between $\frac{2mn}{b+c}$ and $\sqrt{mn}$. In his memoir, "Studien zur Vorgeschichte des Prioritätstreites zwischen Leibniz und Newton um die Entdeckung der höheren Analysis" (Berlin, Verlag der Ak. d. Wiss., 1943), written for specialists, the author reproduces the original texts and Newton's method is expounded. It rests on the consideration of the hyperbola $y=\frac{a}{x}$. The area $\int_m^n y dx = a\log_e\frac{n}{m}$ is used as a first approximation which is afterwards refined. The refinement is a masterpiece of analysis.

The use of modern notation makes these books easier to read. Since our present notation was mainly fixed at the time of Newton and Leibniz, its use introduces little distortion of the actual atmosphere in which they worked. But when, in II, p. 30, reference is made to a partial integration in Wallis's "Arithmetica Infinitorum" (Oxford, 1656), we must be aware of the difference in the background of thought due to a less handy formalism.

* The terms of a "musical" (to-day "harmonic") progression are the reciprocals of the terms of an arithmetical progression.

ON THE GENUS *LYSTROSAURUS* COPE.

By A. S. Brink, M.Sc., Ph.D., Bernard Price Institute for Palaeontological Research, University of the Witwatersrand.

(With three Text-figures.)

(Read April 15, 1950.)

Synopsis.

In this paper "On the genus *Lystrosaurus* Cope", Dr. A. S. Brink gives a revision of the species belonging to this genus. This revision was for some time considered a grave necessity. The twenty-two already described South African species are reduced to eleven species, i.e. *L. andersoni*, *L. bothai*, *L. curvatus*, *L. declivis*, *L. mcCaigi*, *L. murrayi*, *L. oviceps*, *L. putterilli*, *L. platyceps*, *L. rubidgei* and *L. verticalis*, but mention is made that the latter might be a young or female of *L. murrayi*. The three Chinese species, *L. broomi*, *L. hedini* and *L. weidenreichi*, the Indo-Chinese species *L. incicivum*, and the Indian species *L. orientalis* are acknowledged as distinct species. In addition, it is suggested that the generic name *Prolystrosaurus* Haughton should be altered to *Lystrosaurus*, as the former does not form a natural ancestor to this genus. The two species described under the genus *Prolystrosaurus*, i.e. *P. strigops* and *P. natalensis*, bring the total number of already described species of *Lystrosaurus* to eighteen. An additional species is introduced as *L. amphibius*, based on a skull with characteristics pointing more clearly to the aquatic habits of this genus than any other known species.

The first *Lystrosaurus* specimen was described by Huxley in 1859 as *Dicynodon murrayi* (T.S., B.M.N.H., R.1291). In the following year (1860)

Throughout this article the following abbreviations are used:

A.M.N.H. = American Museum of Natural History.
B.M.N.H. = British Museum of Natural History.
B.P.I.P. = Bernard Price Institute for Palaeontological Research.
S.A.M. = South African Museum.
T.S. = Type Specimen.

Owen described three additional species of *Lystrosaurus* under the subgeneric name *Ptychognathus*. These he called *Dicynodon* (*Ptychognathus*) *declivis* (T.S., B.M.N.H., 36221), *Ptychognathus latirostris* (T.S., B.M.N.H., 36222), and *Pt. verticalis* (T.S., B.M.N.H., 36224). Two years later (1862) Owen added a new species to the genus *Ptychognathus*, *Pt. alfredi* (T.S., B.M.N.H., 47342).

The generic name *Lystrosaurus* was used for the first time by Cope in 1870 when he described a specimen as *L. frontosus*. This specimen is at present in the collection of Yale University (No. 2225), New Haven, U.S.A., where it was recently rediscovered by Dr. Broom. The locality is given as "Naup River, 200 miles from Cape of Good Hope". Dr. Broom made a sketch of a transverse section through the skull, which he kindly placed at my disposal.

In his "Catalogue of the Fossil Reptiles of South Africa" (1876), Owen described three new species of *Lystrosaurus*, i.e. *Ptychognathus boopis* (T.S., B.M.N.H., 36253), *Dicynodon curvatus* (T.S., B.M.N.H., R.3792) and *Ptychognathus depressus* (T.S., B.M.N.H., 47064).

In 1890 Lydekker introduced the generic name *Ptychosiagum* for this genus, as the generic name *Ptychognathus* was preoccupied by Stimpson for a Crustacean, and distinguished the following species in the British Museum: *Ptychosiagum declive* (*Ptychognathus declivis*); *Ptychosiagum latirostris* (*Ptychognathus latirostris*, *alfredi* and *depressus*); *Ptychosiagum microtrema* (*Dicynodon microtrema* and *Dicynodon* (*Tropidostoma*) *dunni*); *Ptychosiagum murrayi* (*Dicynodon murrayi* and *copei*, *Ptychognathus verticalis* and *boopis*); and *Ptychosiagum orientale* (*Dicynodon orientalis* and *Ptychognathus orientalis*).

In 1898 Seeley also pointed to the fact that the generic name *Ptychognathus* is preoccupied, but that only Cope's *Lystrosaurus* is valid. He introduced two subgeneric names under the genus *Lystrosaurus*, i.e. *Rhabdocephalus* and *Mochlorhinus*, with the species *R. mcCaigi* and *M. platyceps*, the type specimens of which are in the Albany Museum.

Broom described in 1902 some bones in the appendages of *Lystrosaurus*, but referred the specimen to *Ptychosiagum murrayi*. He used the proper generic name *Lystrosaurus* in 1903 when he described some specimens in the Albany Museum (*L. latirostris*, *L. declivis*, *L. mcCaigi* and *L. platyceps*). In 1907 he introduced a new species, *L. andersoni* (T.S., Natal Museum).

In 1912 Watson gave a fairly complete account of the skeleton of *Lystrosaurus latirostris*, and in 1913 van Hoepen gave a detailed account of the structure of the skull, also of the same species.

A new species was introduced by Haughton in 1915 as *L. oviceps* (T.S., S.A.M. 641), and in the same year van Hoepen introduced the species *L.*

putterilli (T.S., Tvl. Mus.). In the following year (1916) the latter author stressed the necessity of a revision of the genus and at the same time described six new species, i.e. *L. breyeri* (No. 19), *L. jeppei* (No. 15), *L. jorisseni* (No. 17), *L. theileri* (No. 16), *L. wageri* (No. 18) and *L. wagneri* (No. 28). The type specimens are all in the Transvaal Museum.

In 1931 von Huene described additional specimens of *L. alfredi*, *L. depressus* and *L. latirostris*.

Broom, in his "Mammal-like Reptiles of South Africa" (1932), attempted to solve the problem of the growing number of species of *Lystrosaurus* by grouping them all under five species. Under *L. murrayi* he grouped practically all the species and allowed only *Lystrosaurus* (*Dicynodon*) *curvatus*, *Lystrosaurus* (*Mochlorhinus*) *platyceps*, *Lystrosaurus* (*Rhabdocephalus*) *mcCaigi* and *Lystrosaurus andersoni* as additional species. In 1940 and 1943 he proceeded, however, to increase the number again by describing two new species (*L. rubidgei* and *L. bothai* respectively).

Young has thus far distinguished three additional species of Chinese Lystrosauri, i.e. *Lystrosaurus broomi* (1939) = *L. murrayi* (1934), *L. hedini* (1935) and *L. weidenreichi* (1939).

The genus *Prolystrosaurus* was introduced by Haughton in 1917, when he changed Broom's *Dicynodon strigops* to *Prolystrosaurus strigops* and described a new species as *P. natalensis*.

A reorganisation of the species of *Lystrosaurus* has for long been considered a grave necessity. While about to describe a very interesting new species, I thought it advisable to attempt a reorganisation in advance, for which I am in a favourable position with a fair amount of undescribed material in the Bernard Price Institute's Collection at my disposal.

In 1907 Broom suggested that the *Lystrosaurus* species should be divided into two branches, one comprising the smaller types and the other the larger forms like *L. mcCaigi*, *L. platyceps* and the specimen which he then described as *L. andersoni*. To this branch I would like to add van Hoepen's *L. putterilli* and the specimen described by myself as *L. amphibius* in this paper. Furthermore, the species *L. bothai* and *L. rubidgei* may be regarded as ancestral forms to this branch. The characteristic of this branch, distinguishing them from the smaller Lystrosauri, is the height at which the orbits protrude above the level of the dorsal surface of the skull. A series may be presented by the different species of this branch in the following order, starting with the species where the orbits protrude least above the level of the dorsal surface of the skull to the species where the maximum protuberance is found: (1) *L. andersoni*, (2) *L. platyceps*, (3) *L. putterilli*, (4) *L. mcCaigi*, and (5) *L. amphibius*.

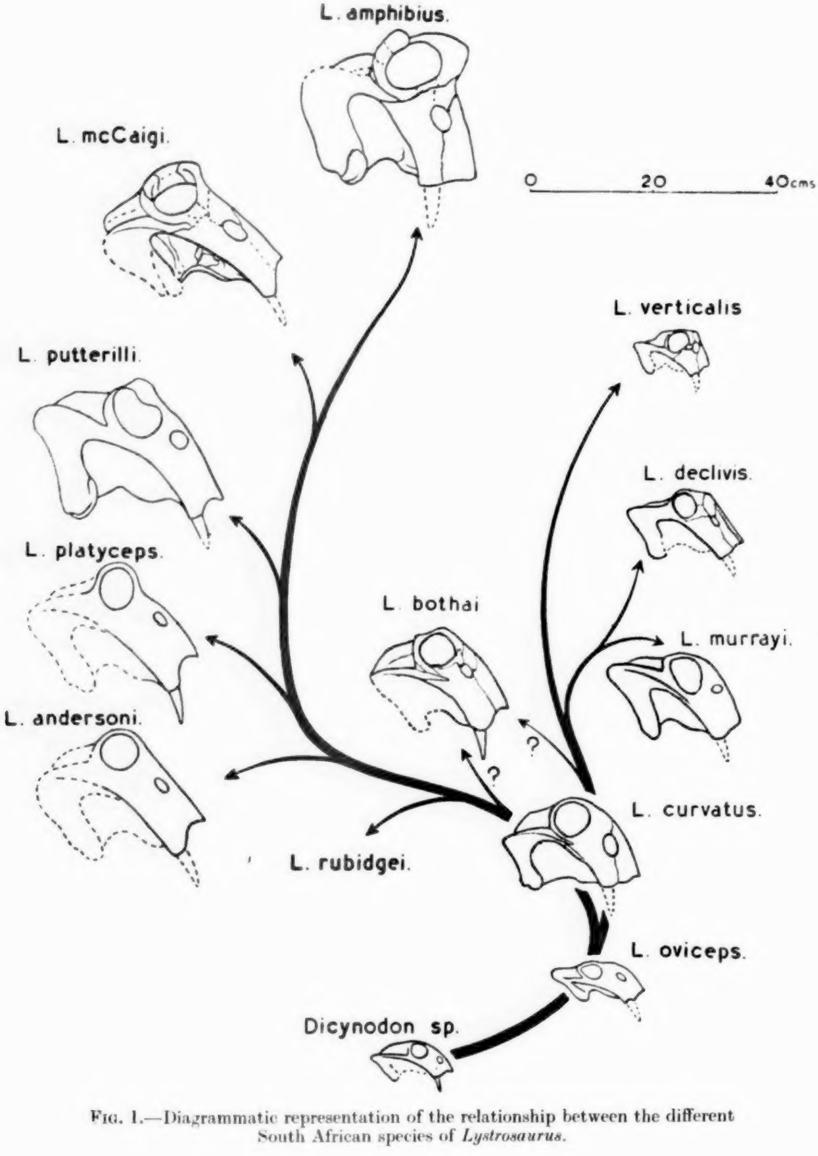

Fig. 1.—Diagrammatic representation of the relationship between the different South African species of *Lystrosaurus*.

The following is an alphabetical list of the species that should enjoy recognition:

Lystrosaurus andersoni Broom.

T.S., Natal Museum: greater portion of a skull. *Locality*: Umkomazan River, Western Natal.

1907. Broom, Report Geol. Surv. Natal, vol. iii, p. 93.

1932. Broom, Mammal-like Reptiles, p. 258, fig. 87B.

The characteristics of the orbits in *L. andersoni* are quite different from those of the following species and there can be little doubt that this is a distinct species.

Lystrosaurus bothai Broom.

T.S., Rubidge Collection: skull. *Locality*: Rygerspoort, Cradock District.

1941. Broom, Ann. Transv. Mus., vol. xx, p. 208, figs. 11, 12.

This specimen appears to be closely related to *L. curvatus*. It differs from the latter species in the greater breadth of the skull and in its more prominent prefrontal bosses on the borders of the orbits. It is quite likely that on account of these prefrontal bosses this species could fall in the branch comprising the larger forms.

Lystrosaurus broomi Young.

T.S. 600065, Cenozoic Laboratory: skull. *Locality*: Sinkiang.

1934. Yuan, P. L., and C. C. Young (*L. murrayi*), Bull. Geol. Soc. China, vol. xiii, No. 4, p. 575.

1936. Broom (*Lystrosaurus* sp. nov.), Ann. Transv. Mus., vol. xviii, pt. 4, p. 402.

1939. Young, C. C., Bull. Geol. Soc. China, vol. xix, No. 2, p. 111.

Young originally described this specimen as *Lystrosaurus murrayi*, but Broom objected on the ground that the lachrymal partly divides the nasal from the prefrontal, a feature not yet found in any South African Lystrosauri. Young consequently referred the specimen in 1939 to *Lystrosaurus broomi*.

Lystrosaurus curvatus (Owen).

T.S., B.M.N.H., R.3792: skull. *Locality*: Cradock.

1876. Owen (*Dicynodon curvatus*), Cat. Foss. Rept. S. Afr., p. 44.

1932. Broom, Mammal-like Reptiles, p. 253, fig. 85A, B.

Specimen 110, B.P.I.P., is a beautiful example of this species. There is no angle between the nasal and frontal or between the frontal and parietal planes; the three regions form a very smooth curve of slightly less than one-quarter of the circumference of a circle. The occipital and parietal

planes form an angle of exactly 90° with each other. The nasal region is smoothly convex from side to side, with no ridges. The frontal region is slightly concave from side to side. The orbits are very large. There is a deep depression over the septomaxillary immediately behind the external nare and in the direction of the orbit. The orbits protrude to a slight extent above the level of the dorsal surface of the skull. The lateral surface of the zygomatic arch is not depressed.

Lystrosaurus declivis (Owen).

T.S., B.M.N.H., 36221: skull. *Locality*: Rhenosterberg.

1860. Owen (*Ptychognathus declivis*), Quart. J. Geol. Soc. Lond., vol. xvi, pt. i, p. 49, pl. i, figs. 3, 4, 5.

1862. Owen (*Pt. alfredi*), Phil. Trans., p. 456, pl. xix.

1876. Owen (*Pt. alfredi, depressus* and *boopis*), Cat. Foss. Rept. S. Afr., pp. 50, 53, 57, pls. xlix, l, li (Rhenosterberg, Stylkrans and Rhenosterberg Resp.).

1890. Lydekker (*Ptychosiagum latirostris*), Cat. Foss. Rept. Amph., p. 35.

1931. von Huene (*L. alfredi*), Geol. Paläont. Abh., Bd. 18, Hft. 3, p. 216, fig. 45 (Naauwpoort).

1932. Broom (*L. murrayi*), Mammal-like Reptiles, p. 244.

This species includes Owen's *Ptychognathus alfredi, depressus* and *boopis*. In 1890 Lydekker placed *L. alfredi* and *depressus* under *Ptychosiagum latirostris* and changed Owen's *Ptychognathus declivis* to *Ptychosiagum declive*. All these species and several others were included under *Lystrosaurus murrayi* by Broom in 1932. Von Huene referred a specimen to *L. depressus* in 1931, but this skull is most likely a *L. oviceps*.

The differences between *L. declivis* and *L. murrayi* are the following: The nasal region is more vertical in the latter than in the former and is much shorter. In *L. declivis* the nasal region is very straight, narrow and high, whereas in *L. murrayi* the nasal region is slightly convex, broad and low. Each nasal has two distinct facets in *L. declivis*. The medial facet is in the same plane as its fellow of the opposite side, but separated from it by a well-definable ridge. A similarly well-definable ridge separates the lateral facet from the maxillary bone of its side. The lateral facet is concave from side to side. In *L. murrayi* the nasal region is more evenly convex from side to side, with no ridges. A more important characteristic defining the species *L. declivis* is the very sharp ridge separating the facial plane from the frontal plane. The frontal plane is flat or concave, and this ridge extends with a sharp convexity forward. There is no such ridge in *L. murrayi*. In *L. declivis* the frontal bosses on the anterodorsal margins of the orbits are developed to a slight extent, whereas they are absent in *L. murrayi*.

Lystrosaurus hedini Young.

T.S. 600067, Cenozoic Laboratory: skull and skeleton. *Locality*: Sinkiang.
1935. Young, Bull. Geol. Soc. China, vol. xiv, p. 483.
1939. Young, Bull. Geol. Soc. China, vol. xix, p. 134.

This specimen compares very well with *L. murrayi*, but differs from the latter in the following aspects: The ridges separating the facial from the frontal planes in *L. declivis* extends straight transversely at the level of the middle of the orbits as in *L. putterilli*. There are also distinct prefrontal bosses of about the same size found in *L. putterilli*. The parietal region is much broader and shorter than in *L. murrayi* and the parietal foramen is broader than long.

Lystrosaurus incicivum (Repelin).

Locality: Indo-China.
1923. Repelin, J. (*Dicynodon incicivum*), Bull. Serv. Geol. Indochine, vol. xii, fasc. ii, pp. 5–7.
1934. Young, C. C., Bull. Geol. Soc. China, vol. xiii, p. 580.

Lystrosaurus mcCaigi Seeley.

T.S., Albany Museum.
1898. Seeley (*Lystrosaurus* (*Rhabdocephalus*) *mcCaigi*), Ann. Mag. Nat. Hist., vol. vii, p. 165.
1903. Broom, Rec. Albany Mus., vol. i, p. 6, pl. i, fig. 3.
1932. Broom, Mammal-like Reptiles, p. 256, figs. 86A, 87A.

This species is easily distinguishable by the height at which the orbits protrude above the level of the dorsal surface of the skull and the slope of the nasal region being less towards the vertical than in almost any other species of *Lystrosaurus*. When considering the slope of the nasal region, the horizontal plane is taken to pass immediately underneath the quadrate condyles and through the necks of the tusks. Unless a specimen of each species of *Lystrosaurus* is dissected and the direction of the horizontal semicircular canal ascertained, it is impossible to say whether this horizontal holds true for the genus or for all the different species, but for superficial purposes of comparison this horizontal plane is of great convenience. It appears also, where in some species the maxillaries are projected downward along the canine tusks, that the necks of the canines are not constant enough features to employ for determining the posture of the skull.

Lystrosaurus murrayi (Huxley).

T.S., B.M.N.H., R.1291: imperfect skull. *Locality*: Colesberg district.
1859. Huxley (*Dicynodon murrayi*), Quart. J. Geol. Soc. Lond., vol. xv, p. 649, pls. xxii, xxiii (Colesberg).

1860. Owen (*Ptychognathus latirostris*), Quart. J. Geol. Soc. Lond., vol. xvi, p. 51 (Rhenosterberg).

1870. Cope (*L. frontosus*), Proc. Amer. Phil. Soc., vol. xi, p. 419 ("Naup River").

1876. Owen (*Ptychognathus latirostris*), Cat. Foss. Rept. S. Afr., pp. 48, 49.

1890. Lydekker (*Ptychosiagum murrayi* and *latirostris*), Cat. Foss. Rept. Amph., pp. 35, 37.

1902. Broom (*Ptychosiagum murrayi*), Trans. S. Afr. Phil. Soc., vol. xi, p. 233, pl. xxiii (Colesberg).

1903. Broom (*L. latirostris*), Rec. Albany Mus., vol. i, p. 3 (Brakrivier).

1912. Watson (*L. latirostris*), Rec. Albany Mus., vol. ii, p. 287, pls. xv, xvi.

1913. van Hoepen (*L. latirostris*), Ann. Transv. Mus., vol. i, pls. ii, iv, vi, viii.

1916. van Hoepen (*L. jeppei, jorisseni, theileri, wageri, wagneri*), Ann. Transv. Mus., vol. v, p. 214.

1932. Broom, Mammal-like Reptiles, p. 244, figs. 80, 81, 82, 83.

The more important characteristics of this species have already been referred to under *L. declivis*.

In 1932 Broom included the six species created by van Hoepen in 1916 under *L. murrayi*. Of these six type specimens I was able to locate three in the Transvaal Museum, i.e. *L. breyeri*, *L. jeppei* and *L. jorisseni*. The former is definitely not a *L. murrayi*; it compares very favourably with *L. oviceps* and I have decided to transfer it to this species. The latter two certainly belong to the species *L. murrayi*, as does *L. theileri*, judging from the illustrations supplied by Broom in 1932. I have unfortunately not been able to trace the specimens described as *L. wageri* and *L. wagneri*, and as no drawings are available, they will have to remain at present under *L. murrayi*, where Broom placed them in 1932.

Lystrosaurus orientalis (Huxley).

Locality: Bengal, India.

1865. Huxley (*Dicynodon orientalis*), Palaeont. Indica, s. 4, vol. i, pt. i, p. 8.

1887. Lydekker (*Ptychognathus orientalis*), Rec. Geol. Surv. India, vol. xx, p. 69.

1890. Lydekker (*Ptychosiagum orientale*), Cat. Foss. Rept. Amph., p. 41, figs. 8, 9, 10, 11.

This species is too imperfectly known to allow satisfactory comparisons with South African forms.

Lystrosaurus oviceps Haughton.

T.S., S.A.M., 641, Tarka River, Cradock District.

1915. Haughton, Ann. S. Afr. Mus., vol. xii, p. 61, pl. xi, figs. 3, 4.

1916. van Hoepen (*L. breyeri*), Ann. Transv. Mus., vol. v, p. 214.

1931. von Huene (*L. depressus*), Geol. Paläont. Abh., Bd. 18, Hft. 3, p. 217, fig. 46 (Ladysmith).

1932. Broom (*L. murrayi*), Mammal-like Reptiles, p. 244.

It has already been referred to that the specimen described by von Huene in 1931 as *L. depressus* is most likely a *L. oviceps*.

L. oviceps is quite definitely the most primitive species of this genus. It points clearly to the origin of this genus from a primitive form of *Dicynodon*. Only in the length of the nasal region and the dorsal position of the external nares does it differ from the genus *Dicynodon*. Its distinguishing characteristic is the gentle curve with which the frontal region passes over to the nasal region, combined with the slope of the latter.

Lystrosaurus putterilli van Hoepen.

T.S., Transv. Mus., No. 196.

1915. van Hoepen, Ann. Transv. Mus., vol. v, p. 70, pls. x, xii.

1932. Broom (*L. murrayi*), Mammal-like Reptiles, p. 244.

The most distinguishing characteristics of this species are the size of the frontal bosses on the anterodorsal borders of the orbits, and the ridge separating the frontal from the nasal region, also found in *L. declivis*, where it extends convexly forward, is extended concavely backward.

Lystrosaurus platyceps Seeley.

T.S., Albany Mus.

1898. Seeley (*Lystrosaurus* (*Mochlorhinus*) *platyceps*), Ann. Mag. Nat. Hist., vol. viii, p. 164.

1903. Broom, Rec. Albany Mus., vol. i, p. 7.

1932. Broom, Mammal-like Reptiles, p. 255, fig. 86B, 87C.

In this species the orbits protrude above the level of the dorsal surface of the skull to about the same extent as in *L. mcCaigi*, but it differs from the latter species in having the nasal plane more convex.

Lystrosaurus rubidgei Broom.

T.S., Rubidge Collection. *Locality*: Bethesda Rd. Station.

1940. Broom, Ann. Transv. Mus., vol. xx, p. 189, fig. 29.

This species resembles *L. platyceps*, but the frontals pass far down on

the facial slope. The prefrontal bosses on the anterodorsal borders of the orbits are fairly large. It appears to fall in sequence between *L. bothai* and *L. andersoni*.

Lystrosaurus verticalis (Owen).

T.S., B.M.N.H., 36224: imperfect skull. *Locality*: ? (Rhenosterberg).

1860. Owen (*Ptychognathus verticalis*), Quart. J. Geol. Soc., vol. xvi, pt 1, p. 54.

1876. Owen (*Ptychognathus verticalis*), Cat. Foss. Rept. S. Afr., p. 50, pl. xlix.

1890. Lydekker (*Ptychosiagum murrayi*), Cat. Foss. Rept. Amph., p. 37.

1932. Broom (*L. murrayi*), Mammal-like Reptiles, p. 244.

This species is the furthest advanced of the branch of smaller Lystrosauri, but is still very close in characteristics to *L. murrayi*. It differs from the latter species only in having a longer and flatter frontal surface, bending down to the nasal surface with a sharper angle, well in front of the orbits. The nasal surface is more vertical than in *L. murrayi*. The skull is also longer and less high.

It is quite possible that *L. verticalis* is a young or female of *L. murrayi*.

Lystrosaurus weidenreichi Young.

T.S. 10.164–10.165, Cenozoic Laboratory. *Locality*: 24, Sinkiang.

1939. Young, Bull. Geol. Soc. China, vol. xix, No. 2, p. 114.

This type is based on a very fragmentary portion of a skull and the larger portion of a skeleton. The structure of some of the bones in the skeleton differ to a reasonable enough extent from any of those of South African forms that I have examined to justify its recognition as a distinct species.

Prolystrosaurus Haughton.

T.S., A.M.N.H. (*P. strigops*); S.A.M. (*P. natalensis*).

1913. Broom (*Dicynodon strigops*), Rec. Albany Museum, vol. ii, p. 400 (Harrismith, O.F.S.).

1915. Haughton (*Dicynodon strigops*), Bull. Amer. Mus. Nat. Hist., vol. xxv, p. 140, fig. 29 (Loskop Natal).

1917. Haughton (*P. strigops* and *P. natalensis*), Ann. S. Afr. Mus., vol. xii, pp. 167, 171, figs. 43, 44, pl. xviii.

1932. Broom (*L. murrayi*), Mammal-like Reptiles, p. 244.

Prolystrosaurus does not form a natural ancestor to *Lystrosaurus*. It is almost certainly further advanced than *L. oviceps*, and ought to be included in the branch of smaller Lystrosauri, near to *L. murrayi*. The generic name *Prolystrosaurus* is, therefore, inappropriate, and I would like

to suggest that the species *strigops* and *natalensis* be referred to the genus *Lystrosaurus*.

Lystrosaurus amphibius sp. nov.

Specimen 136, B.P.I.P., is a large skull, discovered by Mr. J. Kitching on the farm Ripplemead in the district of New Bethesda, Cape Province.

The nasal region is almost vertical, round from side to side, with only a slight longitudinal ridge medially. The prefrontal bosses are very large and

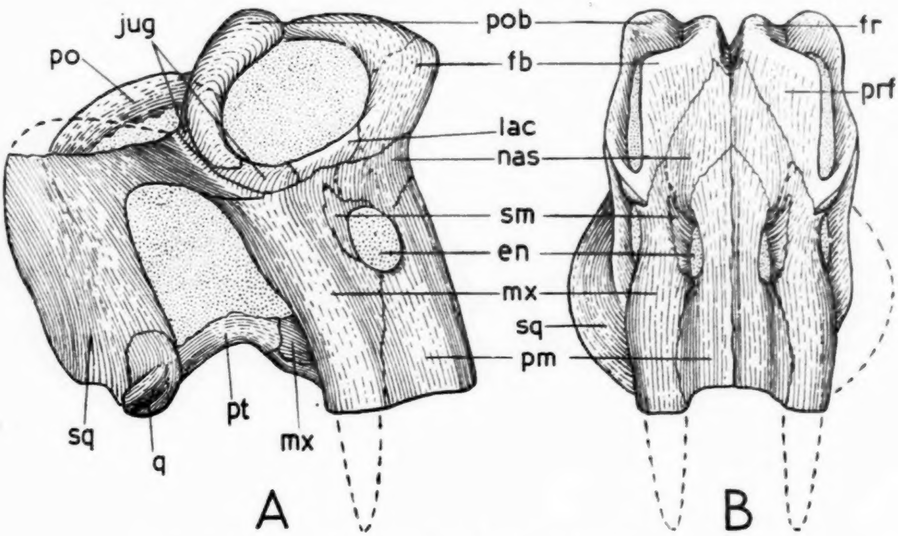

FIG. 2.—A, lateral, and B, anterior, view of the skull of *Lystrosaurus amphibius* sp. nov. (× ¼.)
For abbreviations see fig. 3.

protrude well in front of the level of the nasal plane. In addition to the prefrontal bosses, the postorbitals also form bosses on the posterodorsal margins of the orbits. Between the bosses, on each side, on the dorsal margins of the orbits, is a deep notch. The frontal plane is reduced to a deep groove between the orbits and the parietal plane, which is at the level of the base of the frontal groove, extends upward, forward and sideward on the posteromedial sides of the post-orbital bosses. In the region of the parietal foramen the parietal plane is flat, but short and narrow. The occipital region is deeply depressed, with the squamosals extending backward on each side for a considerable distance. The squamosals approach each other dorsally. The skull is very narrow.

The ventral margin of the external nare is thick. There is no posterodorsal margin to the external nare. The maxillary bone slopes from the region of the lachrymal inward. The depression passes over the septomaxillary into the nasal cavity. The nasal opening, therefore, passes from above downward and inward. The depressions dorsally to the external

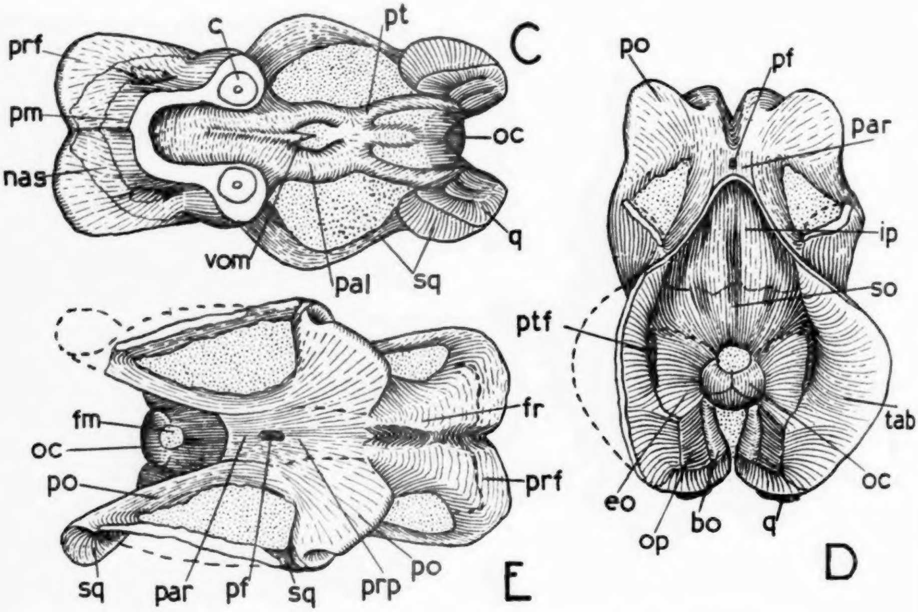

FIG. 3.—C, ventral; D, posterior; and E, dorsal view of the skull of *Lystrosaurus amphibius* sp. nov. (× ½.)

Abbreviations: bo, basioccipital; en, external nare; eo, exoccipital; fb, frontal boss; fr, frontal; ip, interparietal; jug, jugular; lac, lachrymal; mx, maxillary; nas, nasal; oc, occipital condyle; op, opistotic; pal, palatine; par, parietal; pf, parietal foramen; pm, premaxillary; po, postorbital; pob, postorbital boss; pof, postfrontal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; ptf, post-temporal fossa; q, quadrate; sm, septomaxillary; sq, squamosal; so, supraoccipital; tab, tabular; vom, vomer.

nares reach in the direction of the antorbital bosses, the anterior faces of which are shaped in such a way that one cannot reach any other conclusion than that the fleshy nostrils were also directed upward, were attached to these faces, and opened in front of the orbits on the dorsal surface of the skull. These peculiar antorbital bosses are even better shaped for this purpose in *L. putterilli*, and the ridges between the orbits, found in the

latter species and in *L. declivis*, would be of additional service for supporting the nostrils.

Owen already drew attention, in 1860, to the importance of the notch in the posterodorsal angle of the orbit, and suggested that it enabled the animal to turn the eyeballs so as to look upward, or upward and backward. This characteristic, together with the dorsal position of the external nares, the tendency for the orbits to stand as high as possible above the level of the dorsal surface of the skull, and the low position of the mouth, have for a considerable time been regarded as supporting the view that *Lystrosaurus* was aquatic. This new species so clearly demonstrates these characteristics that I wish to call it *Lystrosaurus amphibius*. The notches in the dorsal margins of the orbits enabled the beast to look upward above the water, when the whole body was submerged and only the eyes were at the level of the surface of the water. In this position the nostrils would be above the water.

The following is a list of the *Lystrosaurus* material at present in the collection of the Bernard Price Institute and investigated for this paper:

Lystrosaurus declivis (Owen).

107. A complete skull with lower jaw. Edendale, Middelburg, C.P.
109. A skull with lower jaw, wanting the left zygomatic arch. Elim, Burgersdorp.
118. A snout with the anterior part of the lower jaw. Middelburg, C.P.
123. A complete skull. Honingkrans, Burgersdorp.

Lystrosaurus curvatus (Owen).

110. A complete skull. Edendale, Middelburg, C.P.
114. A complete skull of a small individual. Honingkrans, Burgersdrop.

Lystrosaurus murrayi (Huxley).

106. A complete skull with lower jaw. Edendale, Middelburg, C.P.
111. A complete skull with lower jaw; the posterior portion of the skull is compressed forward. Edendale, Middelburg, C.P.
112. A complete skull with lower jaw. Vlakfontein, Middelburg, C.P.
116. A complete skull with lower jaw. Elim, Burgersdorp.
117. A similar specimen as No. 111. Edendale, Middelburg, C.P.
134. A complete skull, somewhat crushed posteriorly, with lower jaw and skeleton. Harrismith District.

Lystrosaurus oviceps Haughton.

103. Leslie Collection, a complete skull and lower jaw, with the anterior portion of the skeleton.
108. A complete skull with lower jaw. Vlakfontein, Middelburg, C.P.

Lystrosaurus incerte sedis.

115. A very peculiar skull of a new species, but too badly crushed to justify description. Wilgerbosch, New Bethesda.
122. A snout, most likely belonging to the same species as No. 115. Graaff-Reinet District.
113. The anterior portion of a skull (*L. murrayi* ?). Woolwyn, Middelburg.
119. A snout and palate. Middleburg, C.P.
120. A crushed anterior portion of a skull. Woolwyn, Middleburg, C.P.
121. A snout and anterior portion of the lower jaw. Woolwyn.
135. A large portion of a skeleton.

Lystrosaurus amphibius sp. nov.

136. See figures 2 and 3. Ripplemead, New Bethesda.

All these specimens, except No. 103, were collected by the Kitching brothers for the Bernard Price Institute for Palaeontological Research.

THE GEOLOGY OF THE MAKAPAN AND OTHER CAVES.

By LESTER KING, D.Sc., F.G.S., University of Natal.

(With Plates XIII and XIV and six Text-figures.)

CONTENTS.

INTRODUCTION.

The observations recorded herein were made on a visit of three weeks duration to Makapansgat in January 1949, and brief visits to Sterkfontein and to Lobatsi during December 1949. At Makapan, which will be described first, investigation was pursued along three lines: first, a general geological reconnaissance of the district plotted directly on to air photographs, with a more detailed mapping of the Makapan Valley itself (fig. 1); second, an examination of the geomorphology of the surrounding district with special reference to superficial deposits, dongas and assemblages of Stone Age tools therein; and third, an examination of the caves themselves, their evolution, and, where possible, the occurrence within them of fossiliferous rocks of late Tertiary or Quaternary age.

The general geological survey could not, of course, be completed in the time; but much was done, especially by Mr. John Scogings, M.Sc., who accompanied me, and who has subsequently made a mosaic from the photographs.

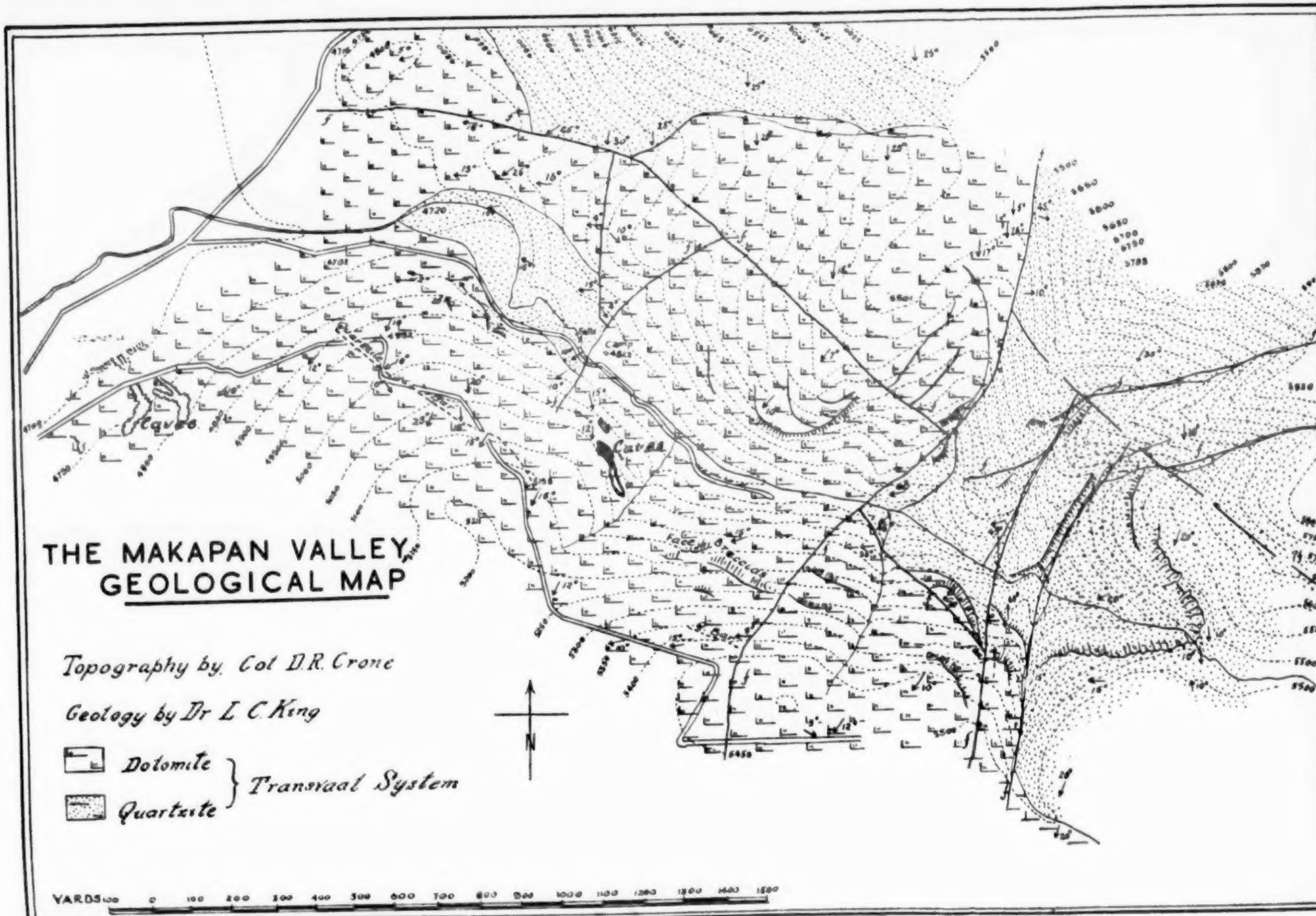
THE MAKAPAN VALLEY
GEOLOGICAL MAP
Topography by Col D.R. Crone
Geology by Dr L C King
Dolomite
Quartzite
Transvaal System
Caves
Caves
Face Breccias
N
YARDS 100 0 100 200 300 400 500 600 700 800 900 1000 1100 1200 1300 1400 1500

Fig. 1.

The second survey involved many miles of donga-crawling, and proved, from the point of view of implementiferous deposits, disappointing. More, however, needs to be done before the study can be regarded as unprofitable.

In the last inquiry, assistance was obtained from the various sections left by the limeworkers who frequently exploited the stalagmitic deposits. The amount of limestone which they removed was considerable and the present form of the caves is, in places, due as much to their industry as to nature. Undoubtedly, in the process of excavation much valuable evidence was destroyed; and one has constantly to visualise not what *is* but what *was* the form of these caves.

Within the past five years (*fide* Mr. G. Peppercorn) the form of Limeworks Cave has been altered by roof-collapse (see fig. 2), the debris of which now blocks a considerable area of the floor.

The Various Groups of Caves at Makapan.

On the farm Makapansgat the caves are all situated in the steep hillsides above the valley floor. Where the valley floor is wide the cave entrances are about one hundred feet above the level of the stream; in the narrow, upper portion of the valley they lie 175 feet above sea-level. If the caves are approximately coeval and were formed by solution acting near stream-level, these figures may afford some measure of stream downcutting since the caves were formed.

It is interesting to note, in this connection, that the various pools of water in the galleries of Peppercorn Cave are now all at virtually the same level, corresponding with the bed of the adjacent Makapan Stream. The underground circulation must here be relatively unimpeded, and a water-table must exist though such is not normal in cave-free dolomite.

The caves, all situated in the Transvaal Dolomite, occur in groups (fig. 3). Nearest the homestead is Peppercorn Cave with three adjacent small caves; half a mile farther up the valley, Buffalo Cave with two adjacent prospect holes; and a mile farther on numerous small prospects. All these caves and prospects are situated in the long, steep hillside that forms the western side of the valley. Nearly all carry red sand deposits, two ages of which are demonstrable (certain fissures having been filled first with a coarse, pisolitic sand and after subsequent re-opening been sealed again with a newer, finer, red sand). Both sands are calcified, the younger commonly less so, but the degree of calcification varies widely with locality. The older sand carries fossil bones at Peppercorn Cave and the younger at Buffalo Cave. Bones appear also in the scattered hillside deposits of the more northerly prospects.

On the opposite side of the valley is the Limeworks cluster of caves;

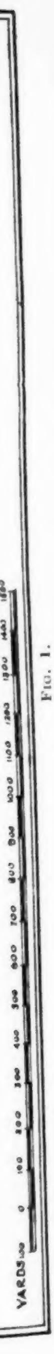

Fig. 1.

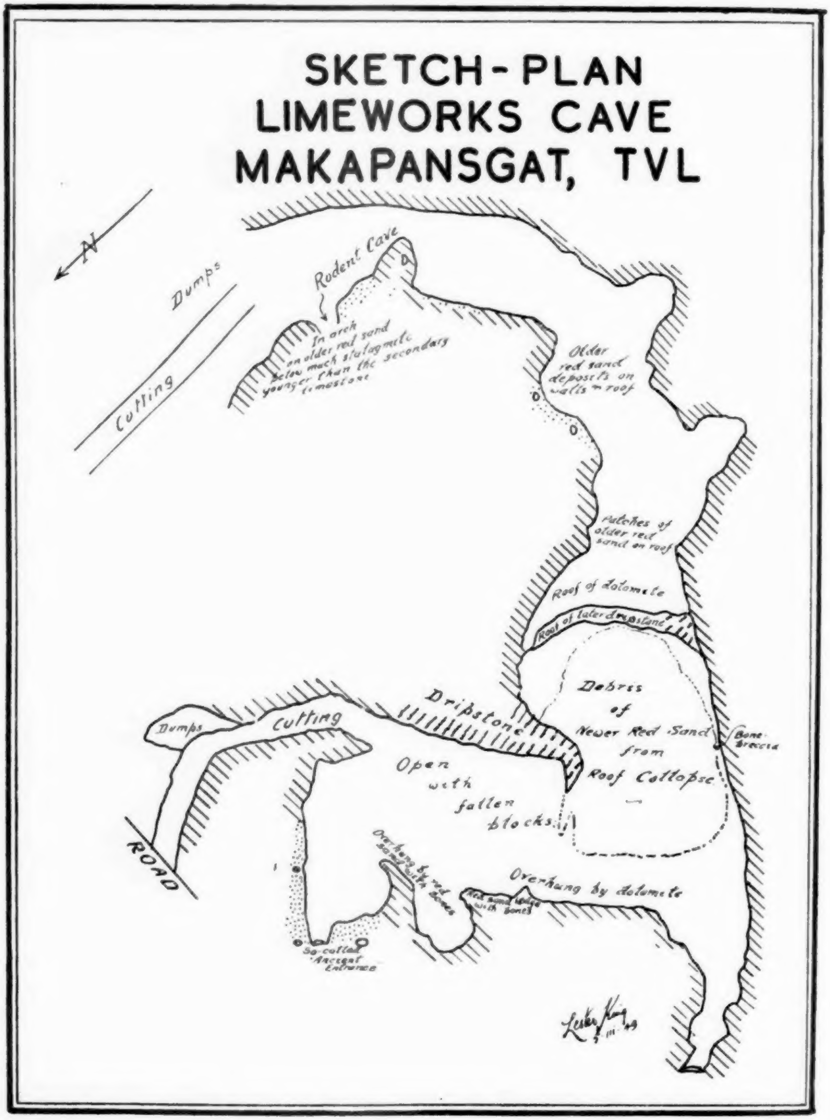
SKETCH-PLAN
LIMEWORKS CAVE
MAKAPANSGAT, TVL
N
Dumps
Cutting
Rodent Cave
In arch on older red sand below much stalagmite younger than the secondary limestone
Older red sand deposits on walls & roof
Patches of older red sand on roof
Roof of dolomite
Roof of later dripstone
Debris of Newer Red Sand from Roof Collapse
Bone Breccia
Dripstone
Dumps
Cutting
Open with fallen blocks
ROAD
Overhung by red sand with bones
Red sand ledge with bones
Overhung by dolomite
So-called 'Ancient' Entrance

FIG. 2.

and farthest upstream, near the hut, the cluster which includes Cave of Hearths, the historic Makapan Cave and Rainbow Cave.

On the neighbouring farm, de Hoop, is a cave in Timeball Hill Quartzite. The entrance to this has been blocked with rubble, stakes, and barbed wire to prevent it serving as a lair for leopards. So far as we could determine, it does not penetrate far into the hillside, but a gang of boys is needed to clear the entrance properly.

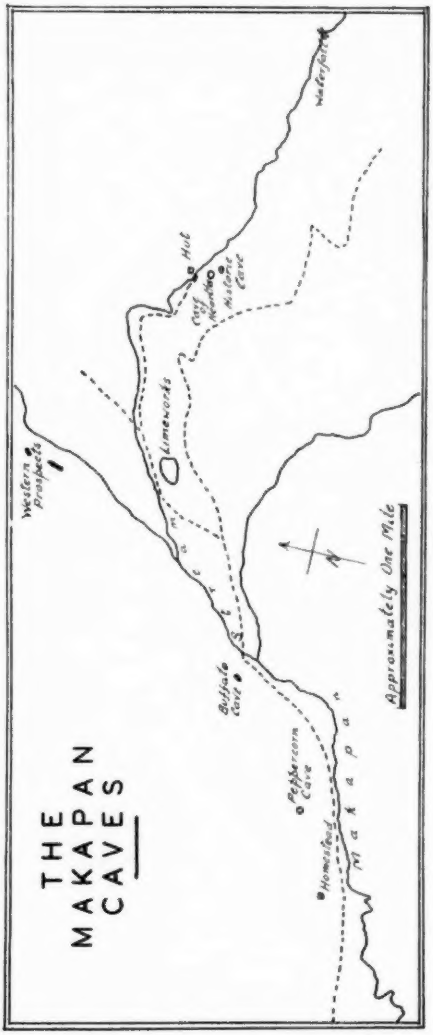

Fig. 3.

The Environment of the Makapan Caves.

All the Makapan caves occur in the Dolomite Series of the Transvaal System. This formation, related to limestone, is soluble in water; nevertheless the caves are seldom in the pristine dolomite, but have been excavated primarily along ancient fractures which have been sealed by deposition in an earlier age of extensive calcite fillings. The fidelity with which the caves follow the calcite breccias (Plate XIII, fig. 1) is sometimes remarkable. In the Peppercorn Cave a straight gallery dissolved along a sealed fracture was followed for 200 yards without the end being reached, and many other instances were noted

covering every one of the groups of caves and prospects. In many situations, excavation by solution has been aided by collapse of the walls and roof, a process which often produces caves sloping "down the dip"; and the historic cave, in which Makapan's people were exterminated by the Boers under Paul Kruger, is, in its present form, wholly due to collapse into some earlier, underlying cavern, doubtless of solutional origin.

The limestone prospectors were well aware of the association of the brecciated zones and stalagmitic deposits in caves, and the hills are dotted with their trial pits wherever the ancient breccia appears. Not infrequently the red sand deposits, with bones, crop out in the vicinity of these prospects and testify the earlier existence of caves or shelters now destroyed by erosion of the hill-slopes.

The rough hills north and east of Makapansgat are composed of underlying Black Reef Quartzite, which is faulted down within the Makapan Valley where it makes the rocky barrier with deep pools which crosses the valley just below the hut (fig. 1). The high falls one mile upstream from the hut are also situated on this formation. The whole area of the valley about the hut has been extensively faulted in ancient times and the country may be correctly visualised as a concourse of fault-blocks.

The multi-stage Pretoria Series, succeeding the Dolomite, is represented first by the Timeball Hill Shale in the stream-bed below the Makapansgat homestead, whence it runs south-eastwards across the open country to be succeeded by the Timeball Hill Quartzites on the farm de Hoop, the lower lands of which are on the Daspoort Shales. The quartzites of the same name follow in sequence as a high ridge with the same south-east strike towards Potgietersrust (Plate XIII, fig. 2).

Apart from superficial accumulations, no other geological series appear within the area studied. The hiatus from Transvaal System to superficial accumulations covers the period from pre-Cambrian to Pliocene.

In the absence of a stratigraphic record some information can be supplied from the geomorphology of the district. The Northern Transvaal was at one time covered by a mantle of Karroo sediments. On this mantle developed the present drainage systems which have since been superposed upon the pre-Cambrian undermass. Thus, back in Gondwana time a mighty plain was developed, the Gondwanaland plain, remnants of which may still be seen upon the Waterberg Plateau to the west, and which passed across the Makapan area equally with the surrounding districts. No trace of this surface remains at Makapansgat. The highlands at the heads of all the streams on neighbouring farms are open and rolling, however, and though not strictly "Gondwana" certainly represent a cycle older than that responsible for the Makapan scenery of the present day, and one probably

not far below the level of the previous "Gondwana" landscape. Most of the highland is, moreover, cut upon the Black Reef Quartzite, which is very resistant to erosion.

The eastern edge of the highland is bounded by a profound erosion scarp which has clearly retreated westward for a distance of several miles under the control of a newer and powerful erosion cycle (the "African" cycle, as at Makapan). At the divide, which is also the crest of the scarp, are numerous water-worn quartz pebbles (as in the stream-valley north of the Makapan).

The "Gondwana" cycle of erosion ended with the development up the rivers and streams of a second erosion cycle (the "African" cycle, which is of Cretaceous to Miocene age at the coast) (King, 1949, p. 444). This cycle penetrated to the Makapan and surrounding districts probably some time in the early Pliocene, having travelled up the Limpopo and the relevant tributary rivers since the early Cretaceous. The streambeds cut cleanly down, sometimes with spectacular results such as the Chunies and other poorts through the Strydpoort Mountains to the east, the great gorges of the Waterberg Plateau to the west, and the valleys of the Makapan and neighbouring streams in the area under review.

In the Makapan hills, the phase of gorge-cutting is still in operation; but downstream, where stream grade has been essentially attained, a further stage of landscape evolution has been reached, namely, parallel retreat of the steep valley sides with the production of broad pediments sloping gently from the base of the hill-slopes to the courses of the streams. It is these pediments which now make the cultivated "lands" of the farm. On the Makapan Stream the change from gorge to open valley takes place about Limeworks. The contrast is accentuated lower down by a passage from the Dolomite to the Timeball Hill Shale, but this is a minor effect, the essential difference being achieved by pedimentation following normal scarp retreat in a new cycle of erosion.

Scarp retreat is expressed in hillside caves chiefly by breaking off of the overhanging lip of the cave. Most of the caves thus have high thresholds of collapsed debris sometimes amounting to talus slopes (Peppercorn, Makapan). The Cave of Hearths has several times broken back in this manner (van Riet Lowe, 1949, pp. 110–111), the debris of earlier falls being associated with red sands and implements of both Early and Middle Stone Age types. Similar deposits doubtless lie buried beneath the threshold debris of other cave-mouths, *e.g.* Buffalo Cave.

At the historic Makapan Cave, formed wholly by collapse into an earlier and lower continuation of the Cave of Hearths, prehistoric remains doubtless lie buried beneath the irregularly-disposed rubble of the modern cave-floor.

Of special interest is the evolution of the mouth of Peppercorn Cave.

Formerly the cave was continuous with the cavity thirty or forty yards to the north-east (fig. 4), the whole system having, possibly, no subaerial outlet. When the small stream (now dry) passing between these two points incised itself, and scarp retreat followed, the connecting roof collapsed. The whole of the distance between Peppercorn Cave and the cavity is thus built of collapse breccia. The break-in is, however, older than the oldest

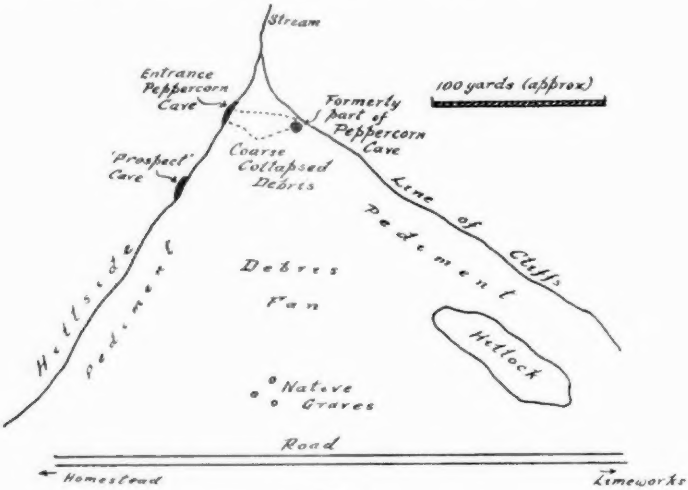

Fig. 4.

of the cave fillings (banded travertine and red sand). Recent retreat of the overhang has built a fresh talus, 70 to 80 feet high, descending into the cave.

The caves are as much an expression of the "African" erosion cycle as are the surficial gorges, pediments and scarps, but whereas the latter are attributable to water flow at the surface, the former are due to flow of water underground. The elevation of the various groups of caves with respect to present stream-beds, and the level of the water-table, coupled with the history of deposition in the various caves (*q.v.*), renders it very likely that the caves are all very closely of the same age. As the erosion cycle arrived in the Makapansgat area about the middle Pliocene, the excavation of the caves is probably of similar date.

The Dongas.

The streams of the Makapan district commonly flow in courses which are incised from 5 to 25 feet below the level of the encompassing alluvia and

pediments. The sides of the dongas are frequently vertical, and as they are composed almost wholly of superficial accumulations (sands, gravels), sometimes bound by calcareous or ferruginous cements, quite impressive sections are often displayed.

Owing to lateral shift of the stream courses during the aggradational phases in which the deposits accumulated, the sections now revealed change rapidly from place to place as the course of the donga is followed. Over many reaches bedrock is seldom seen, appearing only where the streams have cut through the whole of the superficial accumulations. Across the western half of Makapansgat the depth from bedrock is from 12 to 15 feet, but downstream towards Potgietersrust 25 feet is usual.

Some typical sections may now be examined: In a deep donga crossed by the road bridge on the northern boundary of Potgietersrust, gravels and sands of the donga wall are heavily calcified. A short distance upstream the same deposits exhibit no trace of calcification. Quite clearly, calcreting (cementation by deposition of calcite) has operated only where the bedrock consists of rocks rich in the calcium ion such as Bushveld norite, diabase and basic schist (probably an alteration of ancient sediments by the norite). Fissures in the bedrock, too, are here filled with calcrete. But where the bedrock is quartzite, the mantle is usually, though not invariably, free from calcrete.

So far as could be ascertained, enrichment in lime is a result of the prevailing climatic regimen, and no climatic change is necessarily implied by its presence. Naturally, if calcreting is diagnostic of aridity it would appear best over rock rich in calcium, but calcite dusts would be widespread, the waters of even intermittent streams would be charged with lime, and calcreting could be expected to spread widely from the more favoured foci. Calcrete, in arid periods, would be widely distributed over pediments. Indeed, its accumulation is principally a function of leaching, with surficial deposition as soil waters evaporate, and these are processes of the pediment soil mantle.

While one or two limited sections of the donga walls do show local calcification, there has been no universal spread of the process beyond the areas of calcium-rich bedrock, and climatic variation may not be presumed from them alone.

The facts relating to ferricrete are analogous with those for calcrete. In the quartzite poort east of de Hoop farmstead, for instance, there is no ferricrete; but in the shale country downstream towards the fence-line and junction of three streams, the gravels of the donga sides become progressively ferruginised (from the top down) until finally, where the stream makes a plunge pool in the gravels, the full thickness is cemented. Ferricrete, equally with calcrete, therefore, cannot be regarded as a sufficient

indication of climatic change unless widespread (as, for instance, below the Kalahari Sand of Rhodesia); for it, too, is dependent primarily for its occurrence not upon climate but upon the presence of ferriferous rocks.

The presence or absence of gravels, too, is of restricted climatic significance, for gravels are notoriously related to a supply of suitable rock-waste (King, 1948, pp. 217–218). In the Makapan district they occur with clear relation to the outcrops of quartzite or of other hard rocks. There are small barriers at intervals in the donga bottoms, and many of these are attended by "tailings" of derived gravel downstream. Few gravels persist in the donga walls for more than a short distance.

Doubtless, too, much of the gravel in the present stream-beds is derived at second-hand from the gravel beds and lenses of the donga walls, shed into the stream as the walls collapse intermittently on to the donga bed.

Thus it may be seen that, in the Makapan district, superficial deposits vary greatly in type and are largely of restricted local development, and that they show little evidence of profound climatic or regional changes. The following conclusions seem safe:

1. That, subsequent to the Pliocene pedimentation of the landscape in the "African" erosion cycle, a phase of aggradation set in across the lower lands. As will appear, a basal gravel up to 3 feet thick sometimes occurs and this locally contains Early Stone Age implements. Middle Stone Age implements have been found in a second gravel, overlying sands which succeed the basal gravel. Further sands follow, sometimes with lenses of black vlei soils, and the sequence is terminated by modern soils. The whole represents a phase of aggradation with possibly minor breaks, but certainly no great reversal nor erosion of the accumulating mantle.

Whether this stratigraphy is restricted to the Makapan area or is common throughout the Northern Transvaal remains to be decided when other sites have been examined. The history recorded at Rooiwal is not dissimilar. At that site later Middle Stone Age tools have been recovered from a younger series which, near the road-river crossing, lies with unconformity upon deposits containing older Middle Stone Age tools. The basal gravel there again contains Early Stone Age tools.

2. Following the long-continued aggradational phase, the streams have cut deep dongas, in many cases through the full thickness of previous accumulations. This phase is widespread in the Northern Transvaal. In many streams at Makapan the downcutting has been in two stages, with an intervening minor aggradational phase. Following the original excavation of the dongas, the stream-beds were filled in to a depth of 3 to 5 feet with alluvium, and renewed incision has cut a narrow trench through this. This two-cycle downcutting is lost in the lower stream-courses on the farms

Weenen and Planknek where the dongas are vertical-walled often for the full depth of 25 feet (Plate XIV, fig. 1).

The Geology of the Makapan Caves.

Cave geology comprehends two opposed sets of processes: erosion (including solution) which excavates the caves, and deposition (from solution, or more rarely from suspension in air or water) which encrusts or closes up the caves. Both processes may be maintained at the same time. Thus solution at one place may be compensated by precipitation at another, and roof-collapse is soon counterbalanced by cementation of the debris on the floor.

Despite the fact that erosion must earlier be dominant in order that the caves may be excavated, the co-existence of the two opposed sets of processes is real, and the investigator has constantly to bear in mind that quite different phenomena may appear synchronously at points only a few feet distant from one another. The situation presents, as it were, a number of complicated manœuvres by opposed forces which march and counter-march over the same territory with fluctuating fortunes. The results are naturally complex; breaks are frequent and deposits impersistent. Correlation of detail from place to place within a single cavern is often involved, and from cavern to cavern within even a small group difficult or impossible.

If, on the other hand, a correlation can be established, then it must be deemed to have a high degree of probability. Thus the correlation herein proposed between certain banded travertines at Cave of Hearths, Limeworks, and Peppercorn Cave may perhaps later be extended by the demonstration that certain groupings of sand and travertine bands may be matched from cave to cave, as "constellations" of varves are correlated among Pleistocene glacial deposits.

For spelean correlations a geomorphic method, based on stage of development in the cavern cycle, may be employed; or a climatic method based upon fluctuations in the water-table, and the importation of extraneous materials such as wind-blown sands and soils. We shall use chiefly the latter.

Limeworks Cave.

The most complete sequences of spelean formations studied are those evinced in Limeworks Cave and about the Cave of Hearths.

The oldest accumulations within the Limeworks Caves form a set of banded travertine layers, often stained brown by iron oxide from intercalations of red sand. As seen at the so-called "Ancient Entrance" (Plate XIV, fig. 2), the bands are regular though by no means even, the floor on

which the travertine was deposited having been uneven. The deposit suggests a period of cave evolution when ground water had fallen to about the level of the cave floors and when water dripped much more freely than it does now. Maybe there was circulation from pool to pool as in all the western recesses of Peppercorn Cave at the present day. Outside the cave was much blown red sand, and periodically this penetrated into the mouth of the cave, where it spread thinly over the wet travertine surface and became cemented by carbonate. Within the Limeworks Cave the banded travertine continues to the central hall, where it is replaced (*e.g.* at the site marked "Ledge F 1-9") by normal wall-and-floor stalagmite without red sand or banding, and resting upon the dolomite floor.

The banded travertine is succeeded at several stations by ferruginous, occasionally bone-bearing, deposits of red sand. At this stage the caves seem to have dried out and been occupied, for the sands are often calcareous, the calcite having been introduced as dust during the accumulation of the red sand. All gradations exist at Limeworks from siliceous red sand to a limestone rendered only slightly pink by contamination. In all cases accumulation seems to have taken place in the dry state.

Partly by later solution of the underlying travertine, and partly by the excavations of the limeworkers, who found the travertine suited to their requirements, the fossiliferous red-sand deposits usually crop out on the roof of the modern caves, to which they had become cemented. This introduces an important point: the investigator must constantly try to visualise the configuration of these caves at the times of accumulation of the several deposits. Without such a proper conception the interior geology of the caves is meaningless. It has been argued, for instance, that certain of the fossiliferous red sands accumulated so far from the ancient adits that the inhabitants (who may have been *Australopithecines*) must have had some sort of artificial illumination. But this is not necessary. The central portion was then a considerable amphitheatre open to the sky and somewhat larger than the combined orifices of the present day. The sides were extensively overhung, and on ledges and beneath the overhangs accumulated the wind-drifted red sand amid which the bones were incorporated. One occupied portion of the cave, deeper than most, led downwards towards what has been called the "Ancient Entrance". This pocket became filled with calciferous, bone-bearing sands which later became cemented to the roof as well as the floor. The pocket was only 3 to 4 feet high, with the dip on the roof matched by the sloping surface of accumulation of the sand floor; and the noticeable concentration of bones in the lower layers of the deposit surely signifies an abandonment of the pocket by animals as the pocket filled up with sand.

On the western side of the cave, at the site labelled by some previous

investigator "Ledge F 1–9", is another richly bone-bearing deposit, this time of sub-cellular, sand-contaminated limestone. It is this material, herein correlated with the older, bone-bearing sands of the "pocket" above mentioned, from which *Australopithecine* remains are presumed to have come. It lies, as already stated, upon stalagmite, and accumulated to a thickness of 3 or 4 feet. Many long bones are preserved in it, and from it comes also a glassy material that has been ably diagnosed by Bosazza as resulting from fire. The situation was clearly under an overhang, for while the dolomite beneath the bone-bearing sand is unbroken, a few feet away the dolomite is brecciated and much repaired with calcite, suggesting an earlier shortening of the overhang and cementation of the debris by drip from the new edge. This cementation corresponds with the period of travertine formation, and preceeds the older red sand. The sub-cellular limestone itself accumulated as a calcite dust which has since recrystallised. It is to be correlated not with the aqueous stalagmitic deposits, but with the dry-era, older red sands of other parts of the caves.

After a lapsus, a lens of red sand 2 feet thick collected above the sub-cellular limestone, and only subsequently did 4 feet of dripstone succeed. Finally, the local roof collapsed, ending the occupation of this particularly interesting site. The rest of the sequence at this spot ("Ledge F") comprises only 7 to 8 feet of newer red sand (*q.v.*).

To the older red-sand phase succeeded, at Limeworks, a heavy deposition of dripstone (stalactite and stalagmite). This represents the main period of dripstone accumulation within the caves, but at none of the other groups is it so heavy as at Limeworks. Possibly the greater shattering of the Limeworks locality in ancient times, with a concomitant greater quantity of calcite-filled dolomite breccia, provided more calcium carbonate for circulating waters. By contamination with older red sand this dripstone sometimes acquires a pinkish tinge.

The central open amphitheatre was at that time considerably reduced in area by deposition of dripstone (fig. 2), quite different in type from the earlier, banded travertine. The amphitheatre was not entirely closed by the stalagmitic dripstone—many caves remained to be entered by the limeworkers, and on the western side a deep cauldron, one and a half times the cross-section of the recent roof-collapse, remained as a focus for the accumulation of a newer red-sand deposit. It is part of this sand-filled cauldron which has collapsed into the main body of the cave in recent years and which builds the large cone of debris between the two halves of the cave (fig. 2).

The materials of the newer red sand are similar to those of the older red sand; but the formation is seldom heavily calcified and hence is generally loose. Only the lower part is occasionally cemented into breccia, and

contained fossils are rare. There is little sorting, and fine dusts occur with sands and large blocks of rock. The lithology and diagenesis specify a sink-hole environment. Thus in the sides of the collapsed cauldron, 25 to 35 feet deep, a rude stratification, perhaps induced by occasional flooding, shows upon the downhill side; but on the south-east (uphill) side there is no stratification, and the sand is full of angular, fresh and weathered, dolomite blocks, and even some water-worn pebbles. Especially interesting are several pieces of previously-calcified red sand presumably equivalent to the older red sand and derived apparently from the surface round about the cauldron.

In addition to the sands of the cauldron, red, fossiliferous sands upon a ledge in the main cave (fig. 2) may belong to the newer series, but identity could not be established, though clues may later be provided from the palaeontology.

Post-dating the newer red sand in the main Limeworks Caves is a light deposition of stalagmite, best shown along the former tramway leading towards the Rodent Cave. This is sufficiently recent to cover fallen blocks, and in an adjacent cave deposition is still continuing. This neighbouring cave, which forms a continuation of the Limeworks group beyond Rodent Cave and passes beneath the road, contains a sequence strongly confirmatory of that made out at the larger caverns. It comprehends, within the usual country rock of brecciated dolomite, 5 feet of mixed calcareous floor deposits concluding with pool-laid travertine, older red sand (now adhering to the roof) with occasional bones, a newer red sand deposit on the floor of the western part, and, finally, tiny stalactites many of which are curved (helictites). From this "Cave of Helictites" the only phase of the Limeworks sequence that is absent is the dripstone phase, which elsewhere separates the older and newer red sands.

Summarizing, the sequence at Limeworks is:

Modern, tiny stalactites and thin stalagmite;
Newer, mostly sterile, red sand;
Main dripstone;
Older, bone-bearing red sand;
Banded travertine.

One item has not yet been accommodated: the heavily calcified red sand of Rodent Cave. This resembles superficially the older red sand, but the peculiarities of its position, and of its palaeontology—the bones are all of small rodents presumably devoured by owls—render any correlation difficult. It may, of course, represent a distinct phase of sand invasion. Dr. V. L. Bosazza, in an unpublished work which I have been permitted to peruse, states, "In the Makapan Caves there are at least three loesses,

the two lower being hard and carbonated while the highest is somewhat softer", but localities for each are not specified, and, as will emerge in the sequel, *two* red sand phases are present in other caves, *e.g.* at Sterkfontein.

Cave of Hearths and Neighbouring Caves.

From an entrance which is largely artificial, the cave descends "down the dip" in a brecciated dolomite terrain or host rock which is similar in all respects to that of Limeworks. The oldest spelean deposits, which appear in an artificial cave immediately west of Cave of Hearths, are banded travertines deposited on sloping surfaces and much contaminated with red sand. On the west face, indeed, the travertines are replaced by calcified red sands with occasional bones.

The travertines form the floor for an ancient deposit of red sand, richly fossiliferous and heavily impregnated by calcite. As with the older red sand of Limeworks, this deposit is united with the modern roof. No fossil lists have been prepared; but the sand can confidently be correlated upon stratigraphic grounds with the older red sand. The dip of these deposits takes them eastward beneath the floor of Cave of Hearths.

Cave of Hearths showed a floor of dripstone in part contemporaneous with the red sand and in part subsequent. This dripstone was exploited by the limeworkers, whose excavations were partly responsible for the recent collapse of the roof. Doubtless the already deposited older red sand was calcified at this same period of stalagmite formation.

The newer red sand phase is represented by the pinkish cave-mouth breccias and buff sands from which respectively Chelles-Acheul and Middle Stone Age implements have been recovered in a stratified sequence. This formation carried also the Early Stone Age Hearths noted by van Riet Lowe (1938). The matrix of the breccias is a heavily calcified red sand, and the included blocks of dolomite were derived by breaking off of the lip of an ancient cave entrance. Professor van Riet Lowe (1949, pp. 110–111) has described two stages in this breaking back of the lip, affording two sets of breccias associated with the two assemblages of stone tools. Apparently the red sand accumulated semi-continuously throughout the later Early and early Middle Stone Ages. The former deposits were lithified by the abundant drip from the cave entrance, but the Middle Stone Age sands are still partly incoherent.

There is no recent production of stalactites or stalagmite in Cave of Hearths; but as has been explained, the historic Makapan Cave has been formed relatively recently by collapse into a former extension of Cave of Hearths "down the dip". So recent is this engulfment that the joints and other rock faces of the walls and roof are still comparatively fresh, while

the floor consists of irregular debris mounds. Consequently the cave contains no red sand deposits like those of Cave of Hearths. The sole accumulation has been a thin coating of stalagmite, corresponding to the latest phase of Limeworks sequence, in favoured places. This serves to date the collapse as between the newer red sand epoch and the modern thin stalagmite, and completes the Limeworks sequence for the Cave of Hearths–Makapan group.

The sequence may thus be summarized:

Modern, slight local coating of stalagmite;
Collapse, and opening up of Historic Cave;
Newer red and buff sands with implements of Middle Stone Age type:
Breaking back of cave mouth;
Newer red sand with Chelles-Acheul type of implements;
Main dripstone epoch;
Older red sand (on roofs of caves) (*Australopithecine* horizon);
Banded travertine.

The various epochs of deposition are not always so distinct from one another as at Limeworks, and there is more interdigitation between the deposits themselves; but the general correlation may be considered established, though the caves are a mile and a half apart.

Of especial value is the association of both Early and Middle Stone Age implements with the newer red and buff sands, offering two points of sequence for dating on an archaeological basis, and indicating a correlation with what is known in literature as the "Kalahari Sand".

Peppercorn Cave.

The present mouth of Peppercorn Cave exhibits a section of banded travertine layers in all respects comparable with those already recorded at Limeworks and Cave of Hearths. Moreover, succeeding the travertine series is a red sand containing numerous bones and adhering, where the underlying travertines have been removed by lime prospectors, to the roof of the cave. Here, and at a small cave 50 yards south-east of Peppercorn, is, without doubt, the older red sand.

Of the dripstone epoch there is little evidence at Peppercorn Cave, a solitary stalactite in the Bat's Chamber perhaps belonging to this epoch.

Deep within the recesses of the cave, in situations where they could only have been carried by subterranean waters, are loose red sands and clays. No evidence was obtained upon the subject of their age; but their loose state of aggregation suggests that they belong to the newer red sand series.

Bedding is sometimes noticeable, deposition having taken place in quiet underground pools. Bosazza has noted similar clays which "are illite-bearing, and are typical fresh-water clays". There are several pools, all connected, at a slightly lower level in the Peppercorn Cave to-day.

The sands within the cave, far from daylight and laid in water, are naturally barren of fossils; though in the course of exploration two modern antelope skeletons were found in the pools of still water. Evidently the creatures, chased by wild dogs or leopards, had taken refuge in the cave during the night and, fleeing blindly, had penetrated the long gallery, become lost in the side passages, and finally stumbled exhausted into the pools, there to drown. It is conceivable therefore that isolated remains may later be discovered in the sands of the farther recesses.

The latest deposit in the Peppercorn Cave is a foot of bat guano, found in the Bat's Chamber.

Buffalo Cave.

The sequence at Buffalo Cave does not show banded travertine, nor a heavily calcified older red sand on the roof; nor could deposits of the drip-stone epoch be identified. A red sand deposit, calcified in part only, and interpreted as the newer red sand, is plentiful and contains many bones including, according to information received, the remains of a Buffalo. One Middle Stone Age implement was recovered from the upper part of this sand. A light deposit of limestone occurs on fallen debris and is very recent; some is forming now.

Only the latter part of the spelean sequence of Limeworks and Cave of Hearths therefore appears at Buffalo Cave. The cave presents, however, much evidence of having broken back more than other caves, and it is likely that deposits of the earlier epochs, including the older red sand, may be outside at the threshold of Buffalo Cave and lie buried beneath the abundant debris there. This explanation is supported by the extensive apron of heavily calcified red sand in front of the first small cave 100 yards north-east of Buffalo. Such breaking back must have occurred before the Middle Stone Age.

Buffalo Cave is not alone in exhibiting a history which begins with the newer red sand (Middle Stone Age). Rainbow Cave (so-called from its multicoloured hearths) beyond the Historic Cave of Makapan also begins its spelean sequence with this stage, and further removed is Mwulu's Cave (Tobias, 1949, p. 10) in which, yet again, the newer red sand carries a Middle Stone Age assemblage. Even the remote Border Cave (Cooke, Malan and Wells, 1945, p. 8) begins its spelean deposits with this stage, including implements of the Pietersburg culture.

Western Prospect Holes.

In the prospect holes of the western hills, opposite Limeworks, fissures are filled by calcified red sands attributable to two distinct phases of accumulation. The earlier, coarser breccias, sometimes carrying numerous black pisolites, contain few bones mostly of medium-sized buck. Some sands are more like talus or collapse breccias, being filled with angular fragments of dolomite. These are, naturally, sterile.

The northernmost of the prospects displays a cemented fine sand containing only small bones, including an avian pelvis 1 inch long. The deposit is reminiscent of that at the Rodent Cave, Limeworks.

Two phases of accumulation are sometimes noticeable, the filled fissures having opened again after the first sand-filling had hardened. The newer sand is finer, but otherwise undistinguishable, and there is no suggestion that the two phases correspond with the older and newer red sands of Limeworks on the other side of the valley half a mile away. Rather do the sands together resemble the newer red sand of Buffalo Cave, where also black, manganiferous pisolites are common.

The Relation of the Caves to the Environment.

The excavation of the caves, as we have seen, has proceeded in intimate relation to the "African" cycle of erosion which entered the Makapan district probably during the Pliocene period. The caves were apparently dissolved below the level of ground water, and no further excavation has followed the descent of the water-table, except where falls of the roof have occurred. This is in accordance with the normal mode of cave evolution (Davis, 1930, p. 477); but there is no indication of a later period of clay fill (Bretz, 1942, p. 773), probably because the dolomite held little clay and the caves are too near the surface.

Most of the caves display cognate sequences of spelean accumulation, the more nearly complete sequences outcropping nearest the mouths of the caves. This distribution suggests some tens of feet of dripline retreat during the accumulation of the sequence, a conclusion which is supported by the further penetration into the cave system of the newer red sand compared with its older analogue.

The older deposits, the banded travertine and the older red sand, are relics of early opened caves that were filled to the roof inside the entrances.

How long the interval between the accumulation of the two red sands may have been is highly conjectural: it may have been relatively long despite the absence at some stations of major intervening dripstones. The precipitation of dripstone is dependent upon the amount of carbonate-

charged water seeping through the caves, and this in turn upon the amount of calcite available for solution elsewhere in the rocks. At Makapan, the climate has probably never been much more humid than it is now, and now only very little stalactite and stalagmite is forming. Furthermore, the caves are very shallow and the only sources of calcite available for charging the water are the calcite fillings of the ancient dolomite breccias. Hence the paucity and parvitude of the dripstone deposits between the two sand phases does not imply that the time interval between these phases is necessarily short.

At this stage we must examine further the nature and origin of the deposits hitherto called red sands. This term does not exactly designate them, for they are not clean sands but carry much material of the clay grade. "Cave-earth" denotes their physical nature more accurately, but not all the material is of cave origin. They have been called loesses (Bosazza, 1948, p. 228), but for the present the non-committal name of red sands is preferred.

The Red Sands.

The red sands have already been divided into two phases, an older and a newer. The older is more heavily calcified and has been converted into hard rock, whereas the newer is calcified only near the base (Limeworks and Buffalo) and is usually loose and incoherent. While this difference may be partly a function of age, it is likely also that the older red sand contained a higher initial content of calcite dust which has recrystallised *in situ*. At this point we should note that the lithification has taken place not by addition of calcite subsequently to the sand accumulation, but by *recrystallisation of calcite which formed an integral part of the deposit.*

Despite the differences of physical aggregation and age, there is, mineralogically, no marked disparity between the older and newer sands, the second could even be derived from the first. Nor, despite a not unexpected finer grading of materials carried farther into the cave system by subterranean waters, is there any marked mineralogical difference between the sands of the various groups of caves. These concordances tell very strongly in favour of an extraneous origin for the sand materials.

Examination under the microscope reveals plainly that all the sands have a dual origin. Part of the material is of quartz, chert and magnetite, often startlingly angular or even euhedral, which must be of strictly local origin. The chert and magnetite are derived directly from the dolomite, while the angular vitreous quartz is probably from the nearby Black Reef Quartzite. The proportion of these indigenous materials increases, naturally, with the seclusion of the site, but even in the open overhangs they still make the bulk of the deposit.

The minor portion consists of sub-spherical, well-worn quartz grains of remarkably even size, with certain foreign heavy grains of zircon, rutile, pyroxene (of the augite variety), olivine and possibly an amphibole.* The zircon, rutile and amphibole may well be derived from the mass of "Old Granite" on the Pietersburg Road five miles or so to the west, and the pyroxene and olivine from an extensive intrusion of diabase a mile to the south.

The surfaces of the quartz grains, when freed of encompassing iron oxide, are found to be matt or frosted. These grains are typical much-travelled aeolian grains, such as are found in deserts. The presence of such grains poses a question as to their origin. Have they been derived from the local Black Reef Quartzite and been bandied back and forth in a series of local dunes until they were rounded, or have they come from farther afield? And in either case, do they indicate episodic invasions of the Kalahari environment in earlier times?

Bosazza and others (1946) have presented a preliminary statement under this head and have demonstrated the previous intermittent spread of Kalahari conditions farther to the east; and Bosazza has noted that such a statement does not imply that material from the present site of the Kalahari was carried east, but that the Kalahari *environment* spread over a wider area. Much evidence is to hand from Southern Rhodesia, showing that Kalahari conditions formerly extended scores of miles farther to the east, and indeed the vegetation pattern over much of the higher country towards the watershed is still dependent upon the late Kalahari dune patterns (King, 1951). In the Transvaal, conditions must have been essentially akin to those prevailing over similar intervals of time in Southern Rhodesia.

A similarity of sequence from cave to cave does not necessarily imply contemporaneity of deposition. Conceivably, a similar sequence could be exhibited in each cave at similar stages of the spelean cycle of development and deposition (which is very specialised) though the various caves did not pass through the same cyclic stage at the same time. This similarity without contemporaneity might be expected particularly near the mouths of open caves where the influence of "stage" in erosional and depositional effects is especially powerful—and we have already noted that our sequence has been established from deposits never far from the mouths of the caves!

Yet the matter is not really so discouraging. When *alternation* of deposits exists on a pronounced scale, as in the quintuple sequence—banded travertine, red sand, dripstone, red sand, stalactite—it is unlikely that such manifest *reversals* could be achieved by any progressive evolution within the spelean deposition cycle. Stages one, three and five are normal

* I am indebted to Dr. J. J. Frankel for these identifications.

to the cave cycle, the two sand invasions are foreign to it, and record external influences which have temporarily become paramount. Certain elements of the sands themselves are of foreign derivation, possibly far-travelled.

Rapid and small alternations like those within the banded travertine, which is heavily impregnated with red sand, do not, of course, imply any general change of environmental conditions; but rather the co-existence of opposed forces, in this case the red sand accumulating outside and beginning to invade the caves as they were opened to the exterior by hill-slope retreat, as opposed to the fall of the water-table and the precipitation of sheets of travertine inside.

Twice, at least, since the caves were excavated and opened to the outer world, have invasions of quartzose sand swept into the entrances and been trapped therein. Over the surrounding country the same sands have been removed by winds and floods, except where they descended into crevices within the dolomite, where they were retained and calcified. *The sands were apparently supplied in epochs sharply marked off from the times immediately preceding and succeeding them.*

The epochs of wind-drifted sand cannot have been effective only locally, and we may seek to base a correlation of the Makapan deposits on this fact. At the famous localities of Taungs, Sterkfontein and Kromdraai precisely similar carbonated red sands have yielded *Australopithecine* remains. Broom (1946, pp. 141–142) has postulated different ages for these various deposits, but Haughton (1947, p. 58) has suggested that all the *Australopithecine* red sands may be of comparable age. If the red sands were solely the result of the cave cycle, sand could be of any age from Pliocene to Recent; but with the sand supplied in specific epochs, Haughton's view is inherently the more correct. There is no reason why hominids of several types, representing different stages and lines of evolution, should not have existed simultaneously. The younger red sand, which is the next deposit wherein human relics appear, began at Cave of Hearths in the late Early Stone Age and is well developed in the Middle Stone Age, when many other caves (*e.g.* Mwulu's Cave and Border Cave) were inhabited. So the younger red and buff sands seem to have been essentially contemporaneous.

At this stage of the investigation it was evident that data were required from a wider area, and so a visit was later paid to the Sterkfontein Caves near Krugersdorp and to caves near Lobatsi, Bechuanaland.

The Sterkfontein and Neighbouring Caves.

The much-visited Sterkfontein Caves, described by Cooke (1938) as due to solution along two main fissure directions and secondary joint planes,

have acquired special significance through the discoveries of hominid remains made there by Dr. Robert Broom, and it was especially desirable that the Sterkfontein Cave deposits, together with the neighbouring deposits of Swartkrans, Kromdraai and Bolt's Workings, should be linked, if possible, with the Makapan sequence.

Upon examination, the sequence proved to be the same, with two red sands (the earlier with *Plesianthropus*) separated by the main epoch of dripstone formation, and a light deposition of calcite or felting of crystals in conclusion. The banded travertines so characteristic of the base of the spelean sequence at Makapan were, however, nowhere present. The travertines represent a special phase of accumulation—at a time when the caves were opening, and still wet, the red sand blew in from outside. The Makapan caves opened, therefore, after the sand phase had begun outside. The Sterkfontein caves, however, had opened earlier and were already dry before the sand blew in, together with calcite dust which has since cemented it.

At the cave visited by tourists the older red sand appears in the open quarry and in the caves immediately behind and below it. Only in one or two places (Graveyard, and a small side gallery of Milner Hall) did this sand penetrate down crevices to the farther galleries. Of Broom's excavation a description has been furnished by Cooke (1938, p. 204), and though the appearance of the place has altered considerably since, all the various types of deposit which he described are still visible. Cooke's reading of the deposit is, I think, correct: and I visualise the original condition as that of a cave opening outwards, with the lip breaking back and forming a talus, the voids of which were later filled by red wind-blown sand (fig. 5). Towards the former mouth the fallen blocks (up to 1 foot in diameter) are often in contact with one another, showing that they fell before the sand arrived. Farther in, the pieces are not in contact but are embedded in sand which was therefore banking up at about the time these pieces dropped.

This would be the very sort of overhang affording shelter, and facing away from most of the sun's path, which is likely to have been occupied, the inhabitants squatting on the sand and talus, and discarding their meal remnants down the inner slope of the talus which led into the dark caverns "down the dip" back of the shelter. (I have done the same myself at other caves when the rain curtain dripped dismally in front.) The "rubbish tip" at Sterkfontein was filled up by sand as the incursion continued, and in the later phases the skull of "Mrs Ples" was added. Dr. S. H. Haughton has advised me of two water-worn pebbles which he collected at Sterkfontein, and I have seen one other embedded in the talus breccia. These, I think, may have been introduced by the *Plesianthropans*.

The moisture of the dripstone era cemented the whole with the calcite

dust distributed through it, and developed a lens of dripstone at the west end of the quarry where a small pool existed temporarily. The roof still survives above this enclave of the dripstone era.

The chert fragments within the talus breccia often show discoloured weathered rims. These rims, or cortexes, are essentially uniform in thickness (allowance being made for different materials), and this uniformity extends even to similar fragments in other caves. The only conclusion possible is that they have weathered *in situ* buried in the sand; and not weathered at the surface, as has previously been suggested.

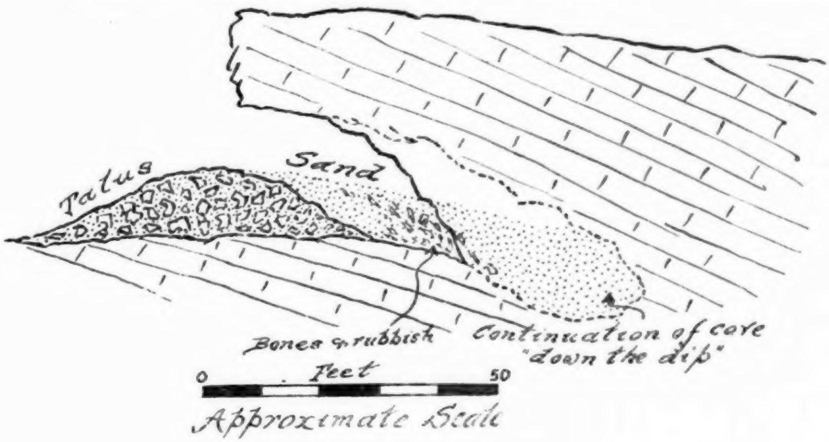

Fig. 5.

In the long cave (one of a group of three) beyond the north-east side of the wire enclosure, stratified older red and yellow sand was evidently laid down in pools. The red variety contains rodent remains; one jaw was identified by Dr. L. H. Wells as probably ***Palaeotomys gracilis*** Broom.

The dripstone era at Sterkfontein ornamented the caves with massive stalactites and botryoidal stalagmite, and doubtless completed the induration of the calciferous sands and "breccias" previously accreted.

The extensive deposits of newer red sand are unconsolidated and generally unstratified. They penetrate much farther into the cave systems than the older red sand, as can well be seen in the caves which lead back, down the dip, from the excavation, though the exposures here are largely covered by quarry-waste. About Bridal Arch and Milner Hall, well within the caves, the sands attain a thickness of 15–20 feet, but this is variable and there is no general levelling of the floor. Following accumulation of the new red sand, parts of the caves have received a light screening of

stalagmite or tiny stalactites. These are, in places, still forming. Several niches and faces are lined with beautiful crystal rosettes, and from the cave beyond the wire, helictites were recovered. Whether crystal growth has ceased could not be determined; but some crystals were recorded to have a light dusting with particles akin to modern soil.

Before leaving the main cave, note should be taken of one especially interesting chamber. The Graveyard is a side-chamber about 80 feet below ground in which apparently all the stages of the history are preserved. The floor and ledge are of unstratified older red sand, with bones and included chert fragments with weathered cortex; this is the only place at Sterkfontein where the older red sand occurs thus far underground, and the manner of its penetration to so secluded a spot offers a pretty problem, the only solution of which seems to be that it came down a fissure which has since been sealed with dripstone. There is, indeed, such a sealed fissure in the roof, but it cannot have been wholly sealed in the dripstone epoch for the newer red sand has also, in reduced quantity, reached Graveyard. It lies below the cemented ledge of older rock (a delightful stratigraphic reversal), and both ledge and floor have subjacent crystal rosettes of the last wet phase of deposition. The newer red sand appears also in a tiny alcove beyond the ledge, where some of it appears to overlie the latest crystal growth, which could only be so if the sand had been held at intermediate level for some time and then descended to the alcove long after the original sand invasion had passed.

The long cave outside the wire on the north shows stratified yellow and red older sand with pebble washes indicating underground stream action. The newer red sand is present, and helictites have been collected among the deposits of the later wet phase. The cave is finally closed by collapse breccia where the roof has fallen in.

At Swartkrans the full sequence is again present, this time in clear stratigraphic succession. The roof of the original cave has long since disappeared following the main dripstone era. The remains of *Paranthropus crassidens*, according to the position indicated by my local guide, came like the other *Australopithecine* remains from the older red sand which locally contains talus fragments. The newer red sand at Swartkrans is stratified towards the base in conformity with the slope of the underlying dripstone. It is sparsely bone-bearing (mostly small bones) and is more consolidated than the newer red sand of Sterkfontein Caves.

At Bolt's Workings, part of the dolomite roof is still in place, and beneath it the two red-sand phases are juxtaposed without the intervention of the dripstone. The older red sand, adhering to the dolomite roof, carries numerous dolomite fragments and abundant antelope remains. This is the deposit worked by the University of California Expedition. The

newer red sand is unconsolidated, crudely stratified, and from it I picked out portion of a jaw, identified by Dr. Wells as that of Burchell's Zebra. The dripstone epoch has left little trace here: it served to cement the old red sand by means of its original carbonate content, and left small travertines in both old red sand and the lowest layers of the new red sand, but there is no heavy stalactite deposition.

I did not visit the famous Kromdraai site, but a specimen of the sand kindly supplied by Dr. R. Broom appears to belong to the older red sand. I do not doubt that the Kromdraai skull which was found about 70 yards away came from the same sand formation despite some difference of matrix.

Neither of the red sands in the caves about Sterkfontein is a residual cave earth. While there are abundant crystals of magnetite and pieces of chert which could be derived directly from the dolomite there are also many mineral grains that appear to be foreign to the dolomite (*e.g.* zircon, tourmaline) and abundant grains of wind-blown quartz.

The results of preliminary heavy-mineral separations are given below (Table I). The older red sands seem to have had fewer minerals per sample, but the range of minerals present is substantially the same for both sands and for the modern soils. Also, most samples of the older sands contain fewer large frosted grains of quartz than the newer, or the modern soils which are, of course, partly derived from the newer red sand. The smaller magnetite grains also are worn and possibly far-travelled, though there are abundant fresh octahedra of local derivation. Zircon is usually fresh, and in the modern soils both zircon and quartz crystals are so fresh as to be doubly terminated. The old red sand is the more heavily calcified and, in both, the grains are heavily coated with limonite. This had to be removed with concentrated hydrochloric acid, to the loss of carbonate and perhaps other minerals.

Admixture in several specimens of newer red sand is indicated by two sharply contrasted grading fractions.

Further research upon these sands by unhurried investigators who can sample systematically and re-check their results in the field is necessary. The present study is no more than introductory.

The Lobatsi Caves.

The hillside caves on the Woodlands Estate near Lobatsi, though lacking a full spelean sequence, have an interest all their own. The two larger caves (fig. 6) are entered by vertical shafts 70 and 80 feet deep respectively, and have clearly been open to the atmosphere for a very much shorter time than the Transvaal caves we have discussed. Neither cave contained the

TABLE I

Locality.	Large, aeolian quartz grains.	Quartz.	Feldspar.	Magnetite.	Zircon.	Rutile.	Garnet.	Amphibole.	Epidote.	Remarks.
Old Red sand, with bones, from roof, side passage between two entrances to Sterkfontein Caves, below Broom's excavation.		×	×	×		×			×	? Tourmaline.
Old Red Sand, with bones, roof of side gallery to Milner Hall, Sterkfontein.	×	×		×						Small crop of heavies. Some magnetite much worn.
Old Red Sand, Swartkrans excavation.		×	×	×		×				Small crop of heavies.
Fine-grained "bone breccia," west corner Broom's Quarry, Sterkfontein Caves.		×		×	×		r			Quartz sand very fine and even grained.
Old Red Sand, Bolt's Workings, Sterkfontein.	×	×	×	×	×				?	Tourmaline, andalusite. Long quartz crystals.
Old Red Sand, Kromdraai.	×	×	×	×	×		r		×	Rare tourmaline. Large wind-blown quartz grains only moderately abundant.
Stratified Old Red Sand, below Yellow Old Sand, cave outside wire, Sterkfontein Caves.		×		×			r	×	×	Material very fine grained, washed far down into cave and waterlaid.
Yellow Old Sand, above Red, cave outside wire, Sterkfontein Caves.	r	×	×	×		×				The few large aeolian quartzes are coated with new crystal.
New Red Sand, 20 ft. thick, at end of lake, Sterkfontein Caves.	×	×	×	×	r		r			Octahedra of magnetite. Some fresh cubes of limonite, pseudomorphous after pyrite.
New Red Sand, Bridal Arch, Sterkfontein Caves.	r	×		×	×		×	×	×	Very few large, wind-worn grains. Pyroxene.
New Red Sand, Bolt's Workings, Sterkfontein.	×	×		×	×		×		×	Andalusite, muscovite.
Pink, banded, New Red Sand, with small bones, Swartkrans.	×	×	×	×	×				×	Small, crystalline quartzes doubly terminated. ? Barite.
Graveyard bone breccia, Sterkfontein Caves.	×	×	×	×	×		×			Material in two sizes. Kyanite. ? Sphene.
New Red Sand, hole behind Graveyard, Sterkfontein Caves.	×	×		×		×		r		Relatively few aeolian grains. Fine grained. ? Barite.
New Red Sand, cave outside wire, Sterkfontein Caves.	×	×	×	×	×	×	r		×	Magnetite octahedra. Many large, rounded quartzes, encrusted with new crystal. ? Octahedrite.
New Red Sand, above dripstone, Swartkrans.	×	×		×		×			×	A dark, bone-bearing variety. Very few aeolian quartz grains.
Modern Soil, dolomite koppie, Sterkfontein Caves.	×	×	×	×	×		×	r		Much coarse chert. Many large aeolian grains of quartz possibly derived from admixture with New Red sand in crevices. Several long, doubly-terminated quartz crystals; much zircon.
Modern Soil beneath former roof, west end Broom's Quarry, Sterkfontein Caves.		×	r	×	×		×		×	No large aeolian quartz grains. Quartz very small. Zircon very fresh, in good crystals.
Modern Soil, Swartkrans.	×	×	×	×	×					All very small in sample except a few wind-worn quartzes.
Soil, drifted down fissures and loose on floor, left-hand chamber before Bridal Arch, Sterkfontein Caves.	×	×		×	×	×				Feldspar not seen.

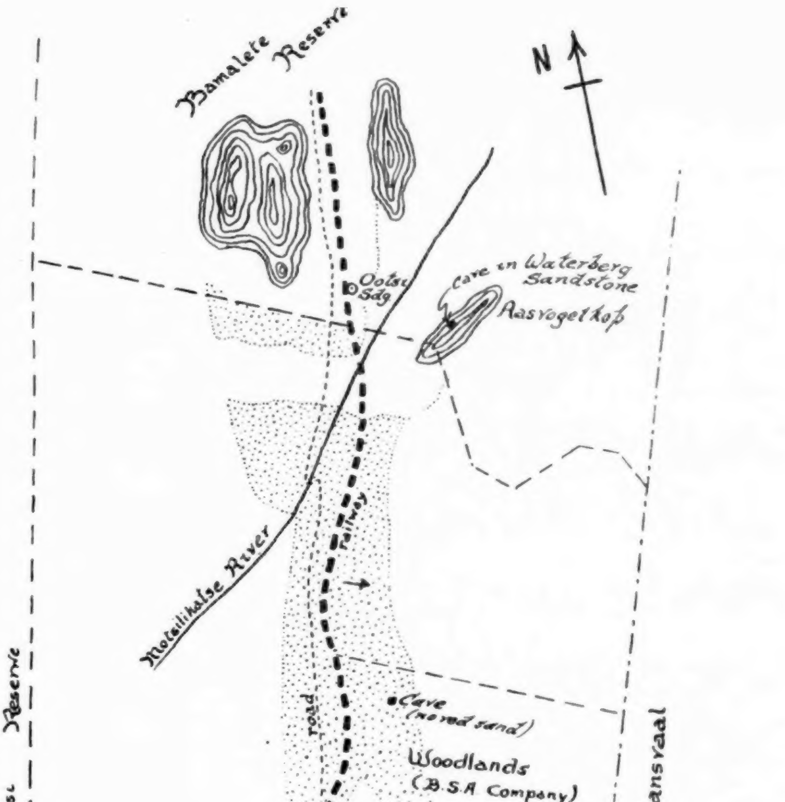
Bamalete Reserve
N
Ootsi Sdg
Cave in Waterberg Sandstone
Aasvogelkop
Motsilikatse River
railway
road
Cave (no red sand)
Woodlands (B.S.A. Company)
Cave (with red sand)
Small Caves
Bangwaketsi Reserve
Lobatsi Block
Transvaal
Geological Survey
Lobatsi Township
Dolomite
Scale
Miles
0
1
2
3
4
5
after Dr. A. Poldervaart

FIG. 6.

older red sand, though both were ornamented underground in the dripstone era. Only one contained the newer red sand; but both contained a late deposit of bat guano, inhabited by ants, scarab beetles, and cockroach-like insects, apparently blind. That the newer red sand should be distributed within a cave which to-day has so small an opening requires the agency of flowing water, but even this does not wholly explain the occurrence.

In the course of one prone crawl along a tunnel, the sand floor was found to be littered with small bones so profusely that they lay upon one another; the place was a regular charnel house, interesting as revealing the conditions which must have existed elsewhere when the fossiliferous sands accumulated. Finally, both Lobatsi caves show a slight deposition of lime at the present time.

At Ootsi, in the Waterberg sandstone, is a cave of different type, a series of curious zigzag dip and joint openings. It contained none of the deposits found in the limestone caves, but we found in the farthest recesses a number of large round native pots said to have been left by refugees from Moselikatse.

Climatic Implications.

The three groups of caves so far examined, Makapan, Sterkfontein and Lobatsi, are established at the apexes of a triangle the sides of which measure 150, 160 and 230 miles respectively. All occur in the landscape of the "African" cycle of erosion, near its encroachment upon the earlier "Gondwana" cyclic landscape, and all except the cave at Ootsi are excavated in the Dolomite Series of the Transvaal. Thus their period and mode of formation must have corresponded. But even more remarkable is the agreement which we have discovered to exist between the deposits which have since been laid in the various members of the three groups of caves. The deposits make a sequence embodying in each case alternating, strongly-contrasted members such as cave dripstones and externally-derived wind-blown sands, and cannot be explained as pertaining to a normal cycle of cave development, whether continuous or interrupted. They suggest a series of climatic controls. The agreement in spelean lithology and sequence over so wide an area prompts also an enquiry into the geographical conditions which formerly existed.

Bosazza and co-authors (1946) have realized that the best approach in the Transvaal is not through the relatively wetter epochs (pluvials) but through the slightly drier epochs when the Kalahari type of environment spread farther to the east. They emphasise that throughout the period covered by these studies the climate has probably never varied very much from a semi-arid mean, and it is precisely under these circumstances that variations of climate, while not affecting greatly the gradients of small

streams nor the pedimentation of the landscape, will, nevertheless, show observable fluctuations of the zone dividing a desert from a "genial" environment.

Bosazza gave a table summarizing the climatic changes which he and his fellow-workers have deduced from cave and other occupational sites of the Transvaal. Except that there is some reason to sink his two phases Kalahari 1 and Kalahari 2 into a single episode, the present study is in substantial agreement with the views set forth in the table. The *Australopithecine* formation corresponds to the older red sand, while late Chelles-Acheul and Middle Stone Age humans correspond with Kalahari stages 3 and 4 of the authors quoted, represented here by long-continuing newer red and buff sands.

Mr. E. J. Wayland, Director of the Geological Survey of Bechuanaland, informs me that the Kalahari sand in the Protectorate carries late Chelles-Acheul and Middle Stone Age implements (*cf.* Victoria Falls and Bembezi Valley of Southern Rhodesia). The later red (Kalahari) sand also correlates with the extensive alluviation seen in the walls of later dongas; and that he also recognises an older, silicified sand which may correlate with the older red, *Australopithecine*, sand of the caves.

The remains of both hominids and humans are therefore associated in the caves with the deposits of the dry epochs. This is partly because those deposits are more suited to the preservation of such relics; but doubtless also the caves were damper during the dripstone epochs and may not have been occupied, though the creatures roamed the veld in the vicinity. The environment in the red sand epochs was doubtless like that marginal to the Kalahari to-day. From the associated bones it is safe to conclude that game was abundant as it is in the Kalahari, where Bushmen still live.

Clearly, subdivision of the red sand phases (which may each occupy considerable intervals of time) is now desirable. This has been achieved in part for the newer red sand by the discovery of Stone Age implements therein, and correlations may later be made with organic remains from the same phase; but for subdivision of the older red sand, this aid is lacking, and subdivision, which seems impossible on lithologic grounds, may to some extent be achieved by palaeontologic study of specimens *meticulously sited in the field*. Museum material is for this purpose useless.

Whatever subdivision of the older red sand may be made in the future, this much is certain, all the Transvaal *Australopithecines* discovered up to 1950 have come from but a single geological formation, and cannot differ greatly in age. The nuances of matrix are due more to differences of situation than differences of age.

The precise age of the older red sand is also not easily defined. None of the methods yet available yields a nearer approximation than Pliocene.

The study of South African cave deposits is in its infancy, and the uncertainties with which we conclude should prove only a spur to further effort. What riches may the next decade reveal?

ACKNOWLEDGMENTS.

For the Makapan study I am indebted to Professor R. A. Dart, the discoverer of Makapan in the palaeontological sense (1925), who first interested me in the geological problems associated with that ancient site; and to Professor C. R. van Riet Lowe, who furnished information relating to Cave of Hearths, which at the time of my visit was much obscured by roof-collapse and by underpinning and packing to support the remainder of the roof. Dr. V. L. Bosazza kindly sent some of his unpublished work for study.

The Bernard Price Palaeontological Institute furnished financial support.

At Sterkfontein, Mr. R. M. Cooper, the owner of the caves, kindly afforded us every facility; and, about Lobatsi, members of the Geological Survey guided us to the caves and helped in the explorations. Dr. A. Poldervaart also supplied the locality map.

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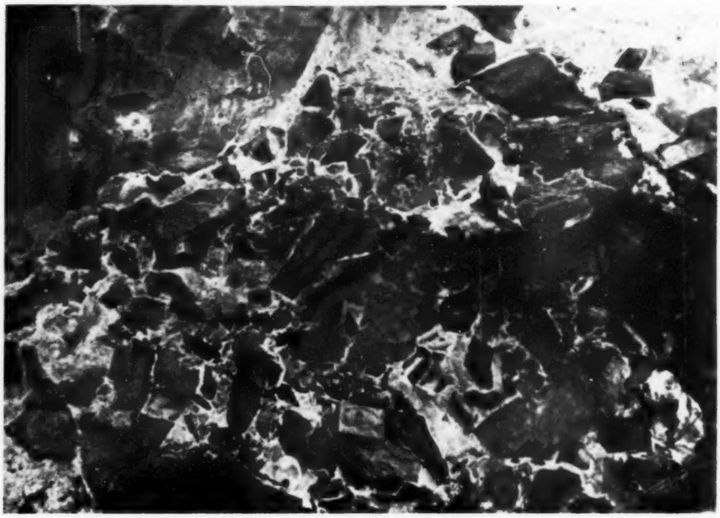

FIG. 1.—Calcite-sealed breccia in dolomite, Makapan.

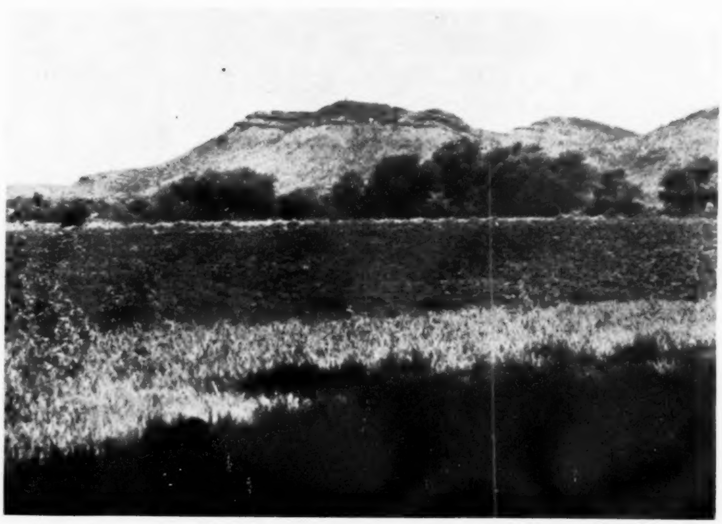

FIG. 2.—Daspoort quartzites in distant ridge, and broad pedimented foreground. Near Makapansgat.

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REPORT ON A SMALL COLLECTION OF MYSIDACEA FROM ESTUARINE WATERS OF SOUTH AFRICA.

By Olive S. Tattersall, B.Sc.

(With twelve Text-figures.)

(Read June 20, 1950.)

I am greatly indebted to Professor J. H. Day of the University of Cape Town for the opportunity of examining this interesting material from estuarine waters of South Africa. These waters have been very little explored in the past, and it is therefore not surprising that this collection consists almost entirely of new species. Of the nine species represented in this material only two, *Rhopalophthalmus egregius* Hansen and *Mesopodopsis slabberi* (van Beneden), have already been described. Six of the remaining seven species, belonging respectively to the genera *Siriella*, *Gastrosaccus*, *Leptomysis*, *Tenagomysis* and *Mesopodopsis* are new to science. Only two specimens of *Siriella* are present. One of them, from Langebaan Bay, is an adult male, and I have been able to describe it in sufficient detail to warrant the institution of a new species. I have great pleasure in naming it after Professor Day. The other is an immature male and is damaged. In view of its immaturity, I have simply figured it and tentatively refer it to *S. australis* Tattersall, which it very closely resembles. Such differences from that species as it shows may be due to its immaturity.

I have pleasure in naming one of the species of *Gastrosaccus* after Dr. I. Gordon of the British Museum, to whom I owe so much for the help and encouragement she has always given me in my work, and in dedicating a species of *Leptomysis* to the memory of my late husband, Professor W. M. Tattersall.

The collections were made mostly by hand-nets or "D"-nets at stations of which I give details below. I have arranged these stations in order in respect of their geographical position, beginning with the most northerly of the east coast stations and passing south and west round the Cape, and have numbered them accordingly. To avoid unnecessary repetition I will refer to them under these numbers in the text which follows.

Details of Stations at which Collections were made.

St. Lucia Lagoon and Estuary on Zululand Coast.

1. St.L. 9F, 3.7.48. Dredged among weed off Charter's Creek.
2. St.L. 12, 4.7.48. Hand-net along shore north of S.A.A.F. Station.
3. St.L. 57B, 6.7.48. Netted near mouth of estuary.
4. St.L. 80C, 15.7.48. "D"-net from west bank between S.A.A.F. Station and Point Island.
5. St.L. 94C, 18.7.48. Hand-net from banks of Upper Bird Island.
6. St.L. 99B, 19.7.48. Near mouth of Nyalazi River.
7. St.L. 102A, 19.7.48. 1½ miles above mouth of Hluhluwe River.
8. St.L. 130, 8.2.49. Collected at 10.20 a.m. off Fanie's Island—no weed on bottom.
9. St.L. 184, 11.7.49. Moonlight plankton, Lake St. Lucia.
10. St.L. 187A, 8.7.49. Moonlight plankton, Lake St. Lucia.

Richard's Bay, North Coast of Natal (Zululand).

11. RH.B. 63A, 3.2.49. Night plankton sample (21.00 hrs.) from channel opposite hotel.
12. RH.B. 63B. Ditto.
13. RH.B. 63C. Ditto.
14. RH.B. 65, 22.1.49. "D"-net in Richard's Bay.

Umkomaas Area about forty miles south of Durban.

15. U.M.K. 18W, 29.1.50. Umzimbazi River. Karridene Mouth of Estuary.

St. John's Area. Cape Province, almost on Natal Border.

16. St.J. 26A (—24H—17B), 19.1.50. "D"-netting at Umgazi (small estuary 7 miles south of St. John's). One mile from mouth—no weed, muddy sand.
17. St.J. 27P, 19.1.50. Under stones in sandy mud near hotel and mouth of Umzimvubu River.

The Haven Area on Transkei Coast between East London and Port St. Johns. The main river here is the Bashee, the Umbanyana is a small stream.

18. HAV. 7T, 13.1.50. "D"-nettings from "Blind Lagoon" at the Haven.
19. HAV. 17D, 14.1.50. In top 2 inches of sand near Umbanyana Mouth.
20. HAV. 2E, 12.1.50. "D"-net in deep water (over 61 feet) near mouth of Umbanyana.
21. HAV. 22B, 15.1.50. Netting in Bashee River at 1st. Kranz.

Hamburg Area. Forty miles south-west of East London.

22. HAM. 10D, 10.1.50. Hand-netting at mouth of Keiskama River—incoming tide.
23. HAM. 10E, 10.1.50. Ditto.
24. HAM. 12, 10.1.50. Hand-netting from main jetty three-quarters of a mile from mouth of Keiskama River at low tide.

Sundays River Area. Thirty miles north-east of Port Elizabeth.

25. SUN. 5B, 7.1.50. "D"-netting from sand flats at mouth of Sundays River.
26. SUN. 5C, 7.1.50. Ditto.
27. SUN. 6D, 7.1.50. About 5 miles from mouth of Sundays River.
28. SUN. 6E and F, 7.1.50. Ditto.

Knysna Lagoon and Estuary. South coast of Cape Province.

29. KNY. 13C, 15.7.47. "D"-net among weed in channel west of Leisure Island (near mouth of lagoon).
30. KNY. 21D, 16.7.47. "D"-net in 3–5 metres from mid-channel opposite Belvedere. About 6 miles from mouth—bottom muddy and covered by loose weed.
31. KNY. 24F, 17.7.47. Hand-net in shallow pools near low-water mark off Leisure Island near mouth of lagoon.

Klein River Estuary and Lagoon near Hermanus.

32. KRL. 24C, 2.5.47. "D"-net in 10 feet of water in middle reaches of estuary.
33. KRL. 27B, 3.5.47. "D"-net in 5–6 feet of water near foot of lagoon in north channel.
34. KRL. 35A, 24.9.47. "D"-net at foot of lagoon in south channel.
35. KRL. 44, 30.5.48. "D"-net in thick weed in upper reaches of lagoon.
36. KRL. 51, 23.9.48. Hand-net at foot of lagoon.

Langebaan Bay. A blind sandy inlet connected to Saldanha Bay on the Cape west coast.

37. L.B. XXA, 15.7.46. Langebaan Bay off Saldanha.
38. L.B. 191H, 26.4.49. Langebaan Bay.
39. L.B. 203H, 28.4.49. Ditto.
40. L.B. 205B & C, 29.4.49. Ditto.
41. L.B. 205P & G, 29.4.49. Ditto.
42. L.B. 211A & B, 26.4.48. Netting from weed on south side.

Berg River Area. St. Helena Bay on Cape west coast.

43. BRG. 10B, 22.9.49. Hand-net in salt-marsh pool at high tide three-quarters of a mile above Laaiplek.

All the specimens from Stations Nos. 27, 30, 32, 33, 34, 35 and 42 and three specimens from Station 14 belong to the species *Rhopalophthalmus egregius* Hansen which has not formerly been recorded from South Africa. The material is well preserved and, in almost every case, in excellent condition. I have therefore been able to confirm W. M. Tattersall's (1915, p. 151) observation on the rudimentary nature of the eighth thoracic endopods in this species and the sexual differences shown by these appendages and to give figures of both sexes (fig. 4, A–B).

Whilst examining this material I noticed that on each side of the first abdominal somite of the males there is a well-developed, very delicate, transparent lamella projecting ventrally to cover the base of the first pleopod (fig. 3A). These lamellae are small in immature males, but no trace of them appears in the females either immature or adult. They have not been recorded by other writers, but, on examining specimens of *R. egregius* from Chilka Lake, India, from Japan and from other localities, and specimens of *R. flagellipes* Illig from West Africa, I find that they are present in all adult males. It would seem that we have here a character of generic significance. It has always been thought that lamellae of this kind on the first abdominal somite were only found in females of members of the sub-family Gastrosaccinae where they form part of the support of the marsupium. Indeed, Hansen (1910, p. 7) states that no other sub-family possesses this character, but it is now evident that it must be included in the definition of the sub-family Rhopalophthalminae.

The other species which make up this collection show very interesting features and add considerably to our knowledge of South African Mysidacea. There is, undoubtedly, a rich field for research in these brackish and littoral waters, and it is to be hoped that it will be possible to make further collections in these areas. In particular, it would be very helpful if further specimens of *Siriella* could be found so that the form of the male pleopods can be ascertained and the new species, at present represented each by a single specimen, more completely described.

ORDER **MYSIDACEA.**

SUB-ORDER MYSIDA.

Family MYSIDAE.

Sub-family **Siriellinae.**

Genus *Siriella* Dana.

Siriella dayi sp. nov.

(Fig. 1, A–F.)

Locality.—Station No. 41. One adult male. 10 mm.

Description.—*Carapace* produced anteriorly into an acutely pointed rostrum which extends to rather less than half-way along the first segment of the antennular peduncle (fig. 1, A). *Antennular peduncle* robust, first

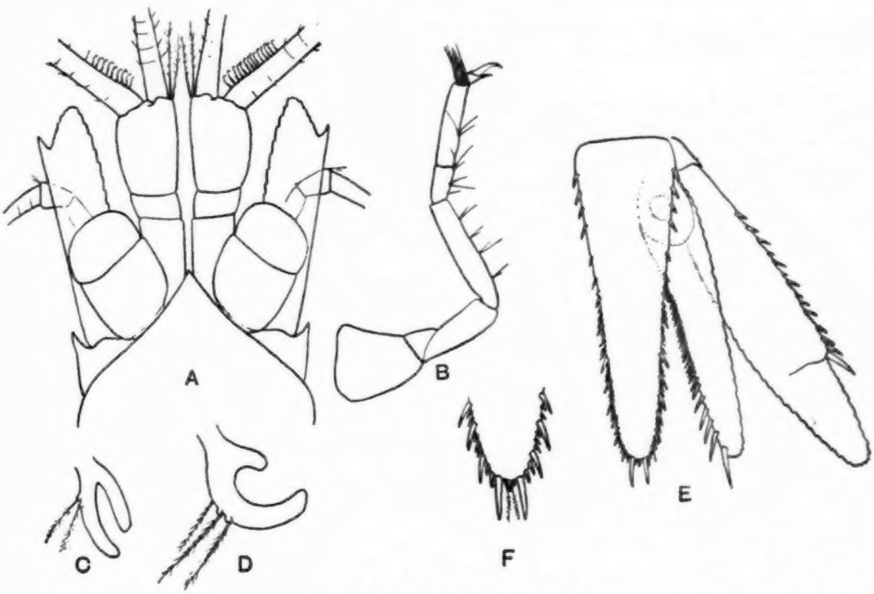

FIG. 1.—*Siriella dayi* sp. nov.

A. Anterior end. × 30.
B. Third thoracic endopod. × 30.
C. Pseudobranchial lobe from first male pleopod. Much enlarged.
D. Pseudobranchial lobe from third male pleopod. Much enlarged.
E. Telson and right uropod. × 30.
F. Apex of telson. × 50.

and third segments subequal; third segment armed on its inner distal angle with two or three long plumose setae. I am not able to see any setae along the inner margin of this segment (fig. 1, A). *Antennal scale* extending slightly beyond the distal end of the antennular peduncle; four and a half times as long as broad; apex produced considerably beyond the thorn terminating the naked outer margin; length of apex equal to the greatest breadth of the scale. The apex is asymmetrical, its most distal point being nearer its inner margin than its outer (fig. 1, A). *Antennal peduncle* slender, about four-fifths as long as the scale. Well-developed spine present on the outer distal angle of the sympod. *Eyes* thick and cylindrical, extending to the distal margin of the second segment of the antennular peduncle, and, when turned sideways, extending considerably beyond the lateral margins of the carapace; cornea occupying more than one-third of the whole organ. *Thoracic appendages* of the typical form found in the genus; carpus small; propodus long and unsegmented; dactylus produced on its distal inner angle so that its distal margin is oblique and armed at this angle with a single strong seta; nail strong and very curved. The distal margin of the propodus is armed with the close row of specially modified setae which forms such a characteristic feature of this genus (fig. 1, B). *Pleopods* with the pseudobranchiae of the first pair nearly straight, of the second to the fourth pairs consisting of two unequal branches which are not spirally coiled but are curved so that they appear like the letter C. The endopod of the third pair is longer than the exopod. Most of the setae are broken off at what seems to be about half their length, but from the appearance of what is left they are not specially modified in any way. Both the fourth pleopods have the exopod quite normal, but the endopod is either broken off or is reduced to a single segment (fig. 1, C–D). *Uropods* with the exopod slightly longer than the endopod and about twice as broad; outer margin of the proximal segment armed along the distal three-quarters of its length with fourteen spines which are somewhat uneven in size and which increase in size distally —the most distal spine is much larger than the others and is very strong; distal segment not quite twice as long as broad. Endopod equal in length to the telson; armed along the inner margin with a very close row of spines which are more spaced on the distal fourth of the margin. I can see no trace of larger spines with smaller ones in the spaces between them, but there is a regular increase in size distally. From the region of the statocyst to about one-third of the length to the apex the spines are so close as to appear actually to touch each other (fig. 1, E). *Telson* long and narrow; more than three times as long as broad at the base; lateral margins nearly straight with no constriction near the base, which is armed on each side with four strong, equally spaced spines; distal spines arranged in series of larger spines with smaller ones in the spaces between them; apical spines very

long; three median spinules present, the middle one slightly larger than the others, but the three do not form a trident such as is found in *S. jaltensis* and several other species of *Siriella*; pair of median plumose setae present (fig. 1, E, F).

Length of adult male, 10 mm.

Remarks.—This species agrees with the description of Hansen's Group II (1910, p. 36) in all particulars except that the pseudobranchiae of the second to the fourth male pleopods are only slightly curved and not spirally coiled. It very closely resembles *Siriella jaltensis* Czerniavsky (of which a very good description with excellent figures is given by G. O. Sars (1877, p. 97, pl. 32, figs. 1–9) under the name of *Siriella crassipes*). The two species resemble one another in the form and length of the rostrum and eyes, in the relative length of the antennular peduncle and antennal scale and in the armature and proportions of the uropods and telson, but they may be distinguished by the following characters:

1. The third segment of the antennular peduncle is much longer and is more robust in *S. dayi* than in *S. jaltensis* and its inner margin does not appear to bear any plumose setae, whereas in *jaltensis* this segment is much shorter than the first and is armed on its inner margin with three (rarely two) long, strong plumose setae.
2. The antennal scale in *S. dayi* is more slender than in *S. jaltensis*, being four and a half times as long as broad whereas in *S. jaltensis* it is less than three times as long as broad; the lateral margins are more parallel, the inner margin being nearly straight and not convex as it is in *jaltensis*.
3. The endopods of the second to the eighth thoracic appendages are more slender and the nail is shorter and more curved distally in this species than in *jaltensis*.
4. The pseudobranchiae of the second to the fourth male pleopods are not spirally coiled but only slightly curved. Czerniavsky (1882, figs. VI, 9–13) figures the pseudobranchiae of the male pleopods of *S. jaltensis* as much less coiled than those shown by Sars for *S. crassipes*, which is now accepted as a synonym of *S. jaltensis*, and it may be that this is a character which changes with age.
5. The spines arming the inner margin of the endopod of the uropod are more closely set and not arranged in series on the proximal part of the margin as they are in *S. jaltensis*.
6. The telson is not constricted near the base and is armed at the base with four spines on each side, while in *S. jaltensis* there is a marked constriction near the base which is armed with only three spines on each side. The median spinules are very nearly equal in size, the

middle one being only slightly longer than the other two and there is no trace of the very definite trident formation so characteristic of *S. jaltensis* and certain other species of *Siriella.*

The form of the third and fourth pleopods of the male is one of the most useful guides in the identification of species of this genus, and it is to be hoped that further specimens of this new species will come to hand so that these appendages may be dissected and fully described and figured.

Siriella species ? *australis* Tattersall.

(Fig. 2, A–B.)

Locality.—Station No. 12. One immature male (damaged). Very dark in colour, nearly black in preserved specimen.

Remarks.—This single immature male measures only 6 mm. and is considerably damaged. All the thoracic endopods are missing, but the telson and uropods are intact and the anterior end, apart from the loss of one eye, is undamaged.

This specimen closely resembles the description and figures of *S. australis* Tattersall (1927, p. 242) except in certain details as follows:

1. The rostrum is relatively longer, extending to within a third of the length from the distal end of the first segment of the antennular peduncle and to more than half the length of the eyes.
2. The antennular peduncle is armed with a strong plumose seta on the middle of the inner margin of its third segment. I cannot see a long stout seta such as is described in *S. australis* on the dorsal surface of the distal margin of the second segment (fig. 2, A).
3. The apex of the antennal scale is shorter and there appears to be a small distal suture present (fig. 2, A).
4. The exopod and, endopod of the uropod are equal in length (fig. 2, B).
5. The spines arming the lateral margins of the telson are larger than those figured by Tattersall for *S. australis* and are less regularly graduated. In the middle region of the lateral margins there is a suspicion of an arrangement in series of larger spines with smaller ones in the spaces between them (fig. 2, B).

Changes with growth are a very usual feature of the members of this genus and, in view of the immaturity of the present specimen, I do not feel prepared to refer it definitely to any known species. Neither do I feel justified in instituting a new species on the evidence it presents. If and

when more material comes to hand, one will be able to decide how far the characters it displays are due to its immaturity or how far they represent reliable data upon which its specific position may be ascertained.

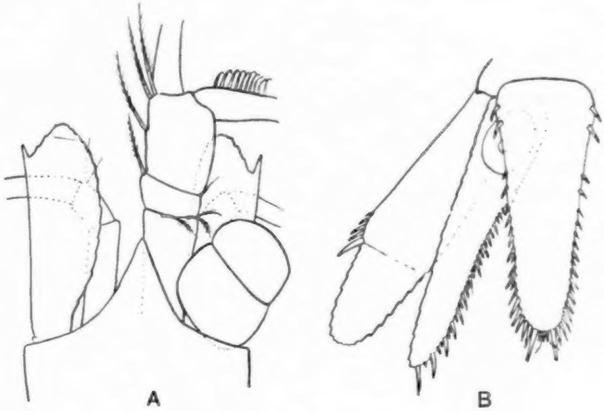

FIG. 2.—*Siriella* sp.

A. Anterior end. ×50.
B. Telson and left uropod. ×50.

Sub-family **Rhopalophthalminae**.

Genus *Rhopalophthalmus* Illig.

Rhopalophthalmus egregius Hansen (Figs. 3, A–H; 4, A–C).

1910. *Rhopalophthalmus egregius* Hansen, Siboga Reports, 37, pp. 48–50, pl. vi, fig. 3, *a–k*; pl. vii, fig. 1, *a–d*.

1915. *Rhopalophthalmus egregius*, Tattersall, "Fauna of Chilka Lake," Mem. Ind. Mus., 5, p. 151.

Localities.—

Station No. 14: Two specimens which had dried up. Station No. 26: Four adult males, 4 juv.; 15 adult females, 8 juv. Station No. 30: Six adult males (largest 15 mm.); 8 adult females with empty brood sacs (largest 17 mm.). Station No. 32: Twenty-five adult males, 4 juv. males; 75 adult females all breeding (13–15 mm.), 77 juv. females. Station No. 33: Two juv. males. Station No. 34: Four adult males (13 mm.); 27 adult females all breeding (13–15 mm.). Station No. 35: Twenty-eight adult males (largest 17 mm.), 32 juv. males; 83 non-breeding females, mostly immature. Station No. 42: One adult male.

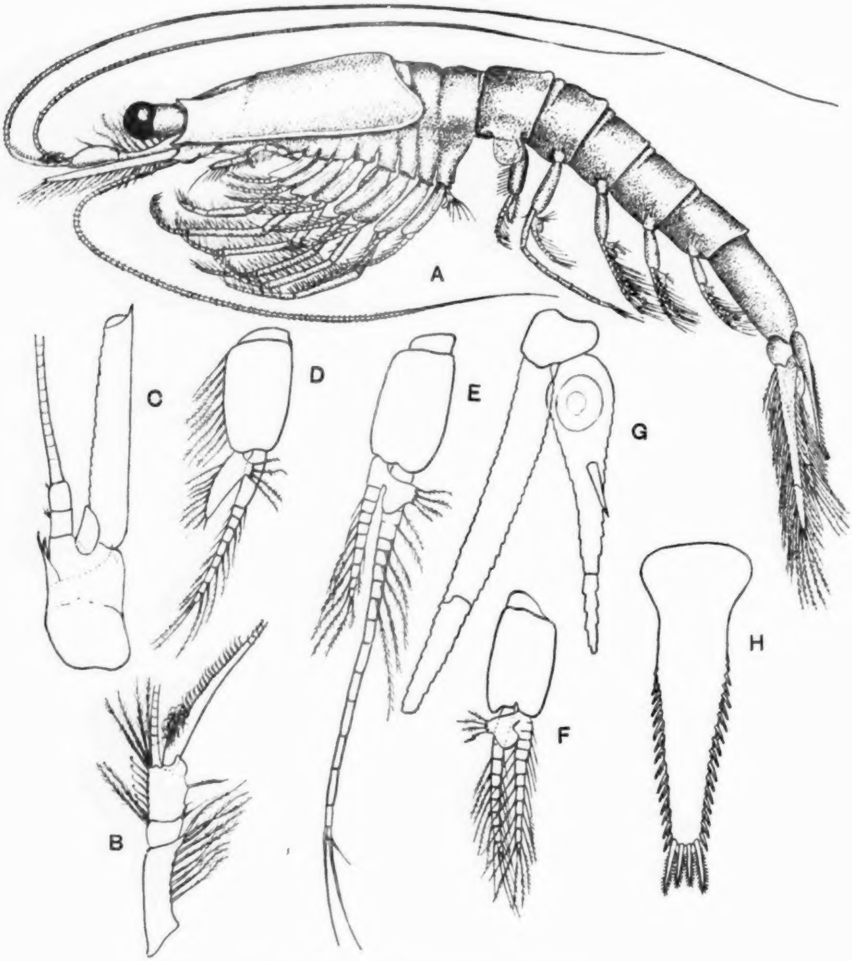

FIG. 3.—*Rhopalophthalmus egregius* Hansen.

A. Adult male. ×8.
B. Antennule of male. ×15.
C. Antenna. ×15.
D. First pleopod of male. ×20.
E. Second pleopod of male. ×20.
F. Fourth pleopod of male. ×20.
G. Uropod. ×20.
H. Telson. ×20.

Remarks.—Only two species have, up to the present, been referred to the genus *Rhopalophthalmus*—*R. flagellipes* Illig and *R. egregius* Hansen. The former can readily be recognised by its very long slender eyes.

R. egregius was instituted by Hansen (1910, p. 48) for a few damaged specimens from Bawaen Island in the East Indian Archipelago. Owing to the mutilated nature of his material, he was not able to describe the thoracic appendages in detail nor the armature of the sympod of the antenna. His specimens had no setae on the outer margin of the exopod of the uropod, but he recorded that this margin was serrulated and suggested that this might indicate that setae had been present but had been broken off.

Tattersall (1915, p. 152), in describing material from India and Japan, recorded that the specimens all had setae on all margins of the exopod and endopod of the uropod, and I have found the same in this beautifully preserved material from South Africa. In these specimens the setae arming the outer margin of the exopods of the uropods are smaller and much more delicate than those arming the inner margin.

Nakazawa (1910, p. 255) recorded this species from Port Shimizu in Japan. He described and figured the very interesting eighth thoracic appendage in which the endopod is reduced to a small, apparently unsegmented vestige which, on closer examination, shows a trace of a suture. The figure he gives is of a female but he makes no mention of any sexual differences in the appendage. Tattersall (1915, p. 151), recording the species from Chilka Lake, India, added details to the description of these endopods and recorded that they displayed sexual differences but gave no figures. I am now able to figure both the male and the female appendages (fig. 4, A–B). The peculiar bent form of the endopod in the male is most characteristic, not only in *R. egregius*, but in all the specimens of *R. flagellipes* which I have seen.

Tattersall, in the same paper, also recorded that the sympod of the antenna was armed on its inner distal margin, at the base of the peduncle, with three long acute spines. In these South African specimens I can only find two spines in this position and a smaller acute spine on the ventral surface at the base of the scale. On the dorsal surface of the sympod between the bases of the peduncle and the scale there is a large, triangular, fleshy outgrowth (fig. 3, C).

The most interesting feature of this species is the presence of lateral lamellae, as described above, on the first abdominal somite of the male. It is surprising that these have not been noticed by earlier workers. Illig's type specimens of *R. flagellipes* were a male of 7 mm. and two immature females. Although he stated that the male was well developed, I think it is probable that it was immature, for Tattersall (1927, p. 315) records males of this species from the west coast of Africa measuring 15 mm.

If Illig's specimen was immature the lateral lamellae would have been very small. Even when fully developed, the lamellae in both species are very delicate and transparent and can easily be overlooked.

The specimens in this collection do show some small points of difference from those from other localities, but I do not consider that they are of sufficient importance to justify the institution of a new species. These

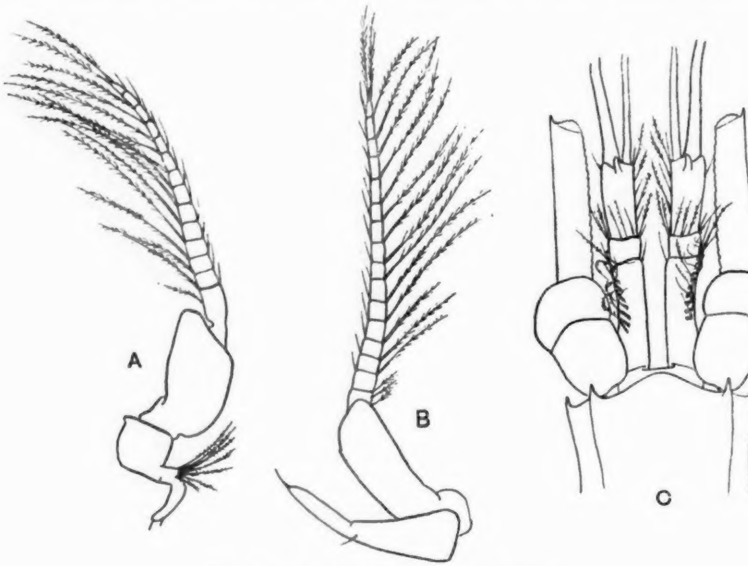

FIG. 4.—*Rhopalophthalmus egregius* Hansen.
A. Eighth thoracic appendage of male. ×25.
B. Eighth thoracic appendage of female. ×25.
C. Anterior end of female. ×16.

differences can best be seen by reference to the accompanying figures. They are as follows:

1. The supra-orbital spines are much larger and run backward along the carapace as definite keels (figs. 3, A; 4, C).

2. The *antennal scale* is longer and more slender, nearly seven times as long as broad; the tooth terminating the outer margin overreaches the very small apex quite considerably; there are only two large spines at the base of the antennal peduncle on the inner margin of the sympod instead of the three recorded by Tattersall, and there is a large, triangular, soft outgrowth on the dorsal surface of the sympod between the base of the scale and the peduncle. This is not mentioned either by Hansen or by Tattersall. There

is also a short, acute spine on the ventral surface of the distal end of the sympod just below the scale (fig. 3, C).

3. The thoracic endopods have the carpus distinct; the propodus divided into six sub-segments in the third to sixth appendages and into seven sub-segments in the seventh. Tattersall records that in the Chilka Lake specimens there are only four sub-segments in the third thoracic limb, five to six in the fifth and sixth limbs, and seven in the seventh.

4. The sympod of the first pleopod of the male is armed along its inner margin with eight to ten long, plumose setae similar to those in species of the genus *Gastrosaccus*. Hansen does not show these in his original figure, and I thought that we had here a definite point of difference. On examining specimens of both species from other localities, however, I find that in all of them the sympod is armed with a number of long plumose setae as shown in fig. 3, D.

Remarks.—This genus may be distinguished from *Gastrosaccus*, which in many ways it closely resembles, in the form of the telson and of the pleopods of the male and in the absence of spines arming the outer margin of the exopod of the uropod. The character by which this genus may be most readily recognised is the entire telson, with four very large spinous spines arming its rounded apex.

R. egregius may be distinguished from *R. flagellipes* by the shorter, comparatively broader eyes and by the presence of a large spine on the endopod of the uropod.

Distribution—

Bawean Island, East Indies. 12 metres. (Hansen, 1910, p. 48.)
Port Shimizu, Japan. (Nakazawa, 1910, p. 255.)
Chilka Lake, India. 4–12 feet. Chiefly among weed. (Tattersall, 1915, p. 151.)
Torres Strait, 10° 35′ S., 140° 13′ E. (Colosi, 1920, p. 237.)
Between New Caledonia and New Zealand, 28° 20′ S., 170° 05′ E. (Colosi, 1920, p. 237.)
Coast of Ariack Sea, Japan. (Tattersall, 1921, p. 408.)
Andaman Isles. (Tattersall, 1922, p. 457.)
Mormugoa Bay, Portuguese India. (Tattersall, 1922, p. 457.)
Madras. (Gopal Aiyah, 1936.)
Great Barrier Reef. (Tattersall, 1936, p. 147.)
Talé Sap, Siam. (Tattersall, unpublished.)
Lake Illawarra, N.S.W. Shallow water. (Tattersall, 1940, p. 330.)

R. egregius is a gregarious form living in swarms at or very near the bottom and is widely distributed in Pacific waters from Japan to India. Its occurrence in the estuarine waters of South Africa considerably enlarges

its known geographical range. It has usually been taken close inshore in shallow and frequently brackish water, but Colosi's record from the Torres Strait and from the open ocean between New Caledonia and New Zealand proves that it is definitely a euryhaline form.

Sub-family **Gastrosaccinae** Norman.

Genus *Gastrosaccus* Norman.

Gastrosaccus gordonae sp. nov.

(Figs. 5, A–I; 6.)

Localities—

Station No. 3: Eight adult and 3 immature males; 7 adult and 2 immature females. Station No. 36: Two adult males; 7 adult and 2 immature females. TYPES.

Description.—General form similar to that of *G. sanctus*. *Carapace* with anterior margin produced into a very short obtuse angle; antero-lateral angles somewhat produced into a bluntly rounded right angle. Posterior margin emarginate, leaving the eighth thoracic somite and part of the seventh exposed in dorsal view; a small inwardly directed lobe present on each side close to the median line. There is also, on each side of the emarginate posterior margin, a notch with overlapping, rounded edges exactly similar to that seen in the same position in *G. sanctus* (figs. 5, C; 6). *Abdomen* somewhat laterally compressed especially in the region of the fifth and sixth somites. No trace of a median dorsal spine on the fifth somite; sixth somite equal in length to the telson. *Antennule.* First segment of the peduncle slightly shorter than the second and third segments combined; second segment well developed, with three stout spines set obliquely along its outer margin. This appendage is very similar to that of *G. sanctus* G. O. Sars (1877, p. 64, pl. 22, fig. 1; pl. 23, fig. 2), but the three spines arming the secohd segment are smaller and not set so obliquely in that species as in *G. gordonae* (figs. 5, A; 6). *Antennal peduncle* extending forward to the distal end of the second segment of the antennular peduncle; second segment stouter and more than twice as long as the third. *Scale* very small and slender, extending only to the middle of the third segment of the peduncle; four times as long as broad; rounded apex extending only slightly beyond the thorn terminating the naked outer margin; a small distal suture present (fig. 5, B).

Thoracic appendages similar to those of *G. sanctus*. *First pleopod of male*: Outer margin of sympod armed with ten to twelve extremely long and very plumose setae; *endopod* very short, unsegmented, armed with about five

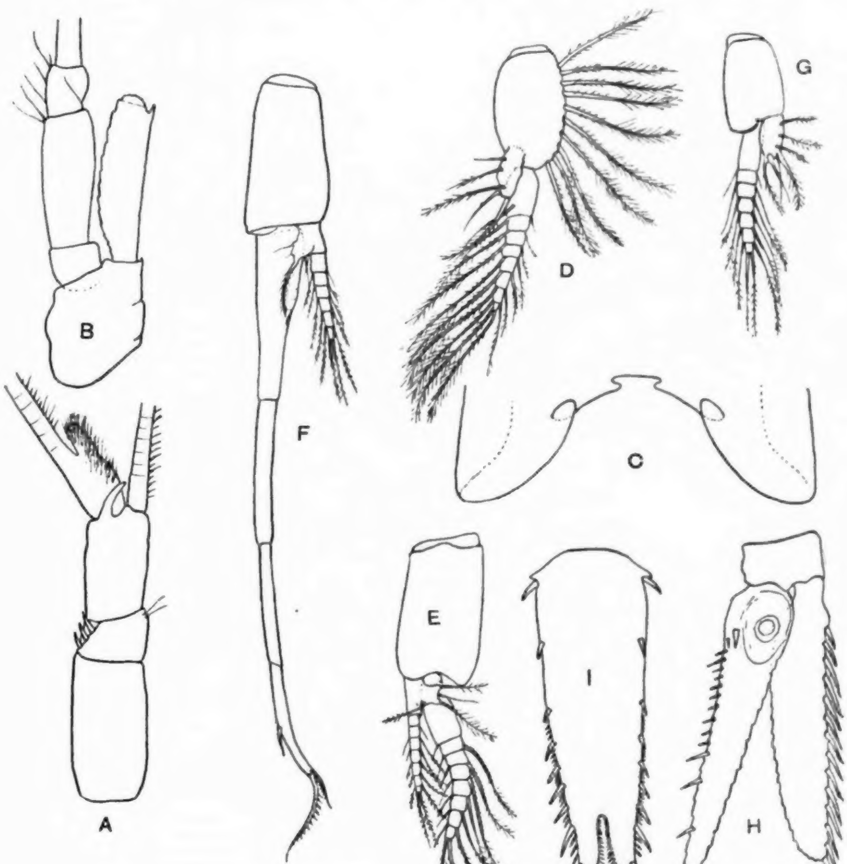

FIG. 5.—*Gastrosaccus gordonae* sp. nov.

A. Antennule of male. × 37·5.
B. Antenna. × 37·5.
C. Dorsal view of posterior margin of carapace. × 22·5.
D. First pleopod of male. × 42·5.
E. Second pleopod of male. × 42·5.
F. Third pleopod of male. × 42·5.
G. Fourth pleopod of male. × 42·5
H. Uropod. × 37·5.
I. Telson. × 22·5.

plumose setae of which the most distal is particularly long and strong; *exopod* composed of eight segments of which the first is the largest; the plumose setae arming the inner, distal corners of the segments are much longer, stronger and more densely plumed than those arming the outer corners (fig. 5, D). *Second pleopod of male: Endopod* slender, shorter than the sympod; composed of eight segments with a well-developed pseudobranchial lobe present on the basal segment. *Exopod* robust, more than twice as broad as the endopod and nearly half as long again; plumose setae of outer margin much larger than those of inner. The setae on the outer distal corners of the second to the fourth segments are modified, being thickened and having their proximal margins serrated. A similar modification has been described for these setae in *G. kempi* Tattersall (1922, p. 460), but the serrations do not extend so far along the setae as in *G. gordonae* (fig. 5, E). *Third pleopod of male: Exopod* very long, extending backwards to the proximal end of the telson. It is composed of four segments. The first segment is longer than the second; the third and fourth segments are subequal and shorter than the second; fourth segment armed midway along its outer margin with a strong simple seta and terminating in two long, unequal, barbed setae. *Endopod* well developed, seven-segmented; basal segment longer than the others and bearing a well-developed pseudobranchial lobe which is armed with four small setae and, at its tip, a very long, strong, plumose seta which extends to three-fourths of the length of the whole endopod (fig. 5, F). *Fourth and fifth pleopods of male* similar to those of *G. sanctus* except that the setae arming the small, unsegmented endoped are very much longer and stronger than those figured by Sars (1877, pl. 23, fig. 8). The exopod is composed of seven segments (fig. 5, G). *Uropod* subequal in length to telson; *exopod* armed on outer margin with fourteen strong, regular spines which are finely plumose along their inner or distal margins; *endopod* very slightly longer than exopod; armed at the inner side of the statocyst with two posteriorly directed spines, the one nearer the statocyst being about three times as large as the outer one. The inner margin is armed with a row of ten small, unequal spines extending from the statocyst to half-way along the margin; distal half of margin armed with three very long, widely spaced spines (fig. 5, H). *Telson* three times as long as broad, and cleft to about one-fourth of its length; lateral margins armed with nine large spines, the spaces between the third to terminal spines being occupied with three to six small, regularly graduated spinules. The spinules are more numerous and smaller in the more proximal spaces. Apical spines long and strong, one-twelfth of the total length of the telson. Cleft armed with twenty to twenty-five teeth on each side (fig. 5, I).

Length of adults of both sexes, 9 mm.

Remarks.—This species resembles *G. kempi* Tattersall (1922, p. 460) in

general form and in the form and armature of the male pleopods and telson. *G. kempi* was until now the only species of the genus to be described with the spines arming the lateral margins of the telson arranged in series of larger spines with smaller spines in the spaces between them. The telson of *G. gordonae* is almost precisely like that figured by Tattersall for *G. kempi* except that it is longer and narrower and its apical spines are smaller than in *G. kempi*.

The endopod of the third pleopod of the male of *G. gordonae* is composed

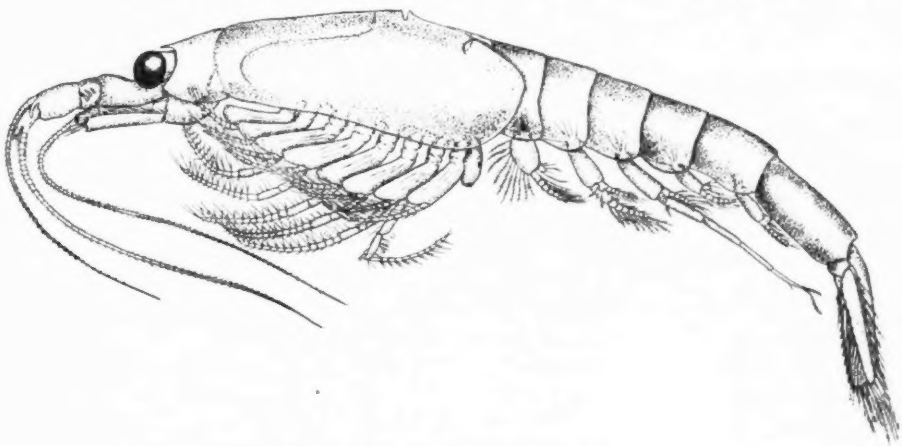

FIG. 6.—*Gastrosaccus gordonae* sp. nov.
Adult male in lateral view. × 15.

of seven segments, while in *G. kempi* there are only six. The basal lobe is armed with some small setae and one very large strong plumose seta at the distal end. According to the figure given by Tattersall for *G. kempi*, the basal lobe bears only a few small setae and no specially long one. The proportions of the four segments making up the exopod of the third pleopod of the male in *G. gordonae* differ from those of *G. kempi*. In the former species the third segment is the smallest and the distal segment is equal in length to the second, while in the latter the four segments become progressively shorter distally.

The main character which serves to distinguish *G. gordonae* from *G. kempi* is the presence of small, inwardly directed lobes in the middle of the posterior margin of the carapace (figs. 5, C; 6). For many years it was thought that *G. normani* had no upturned lappets on the dorsal hinder margin of the carapace and that their absence served as a reliable guide for the identification of the species. It has now been proved that rare individuals which are

undoubtedly *G. normani* possess upturned lappets similar to those found in *G. sanctus*. It may be that the examination of further material will show that the small lappets on the posterior margin in *G. gordonae* are not always present, but in all the specimens in this collection the carapace is as figured (figs. 5, C; 6). I have therefore decided that there are sufficient grounds for the institution of a new species for these specimens, and I have great pleasure in associating it with the name of Dr. I. Gordon.

Gastrosaccus brevifissura sp. nov.

(Figs. 7, A–E; 8, A–J.)

Localities.—

Station No. 9: Eight juv. Station No. 11: One male. Station No. 13: One male, 1 female. Station No. 19: One male. Station No. 22: One juv. Station No. 23: Five adult males (11–11·5 mm.), 4 juv. males; 2 breeding females (11 mm.), 2 non-breeding females, 2 juv. females. Station No. 25: Twenty-five males, 21 females (about 50 per cent. are immature). Station No. 38: One adult male, 2 adult females, 2 juv. females. Station No. 40: Twenty-one adult males (largest 11·5 mm.), 2 juv. males, 57 ovigerous females (largest 12 mm.). Types. Station No. 41: Six adult males, 2 juv. males, 1 adult female, 2 juv. females.

Description.—*Carapace* very short anteriorly, leaving the eyes completely uncovered; rostrum short and acutely rounded; posterior margin with two flat, rectangular, backwardly directed flaps close to the median line; median portion of carapace between the flaps transverse and not produced (fig. 7, A–B). *Abdomen* robust and not noticeably compressed laterally in the region of the fifth somite; posterior margin of fifth somite produced so that in lateral view it appears like a short strong spine; sixth somite much more slender than, and about half as long again as the fifth (fig. 7, C). *Antennular peduncle* with the first segment equal in length to the second and third together; second segment armed on its outer margin with three strong spines and on its inner distal angle with a single long, strong plumose seta. The outer flagellum is swollen on the inner side of its base, and the swelling is armed with a close regular row of long strong setae. In the male the distal portion of this swollen area is enlarged and covered thickly with dense, fine curling setae (fig. 7, A). *Antenna* small, scale short, extending only to the distal margin of the first segment of the antennular peduncle; tooth terminating the naked outer margin slightly longer than the apex of the scale; a very small distal suture present (fig. 7, A). *Labrum* produced anteriorly into a long sharp point.

Thoracic appendages similar to those of *Gastrosaccus sanctus* (see G. O. Sars, 1877, pls. 22–23). The large basal segment in the first to seventh pairs of appendages is armed on its outer distal corner with a strong tooth.

In the eighth pair of appendages this angle is smoothly rounded. Genital appendage very large, somewhat conical in shape and terminating in a small triangular flap (fig. 7, D–E).

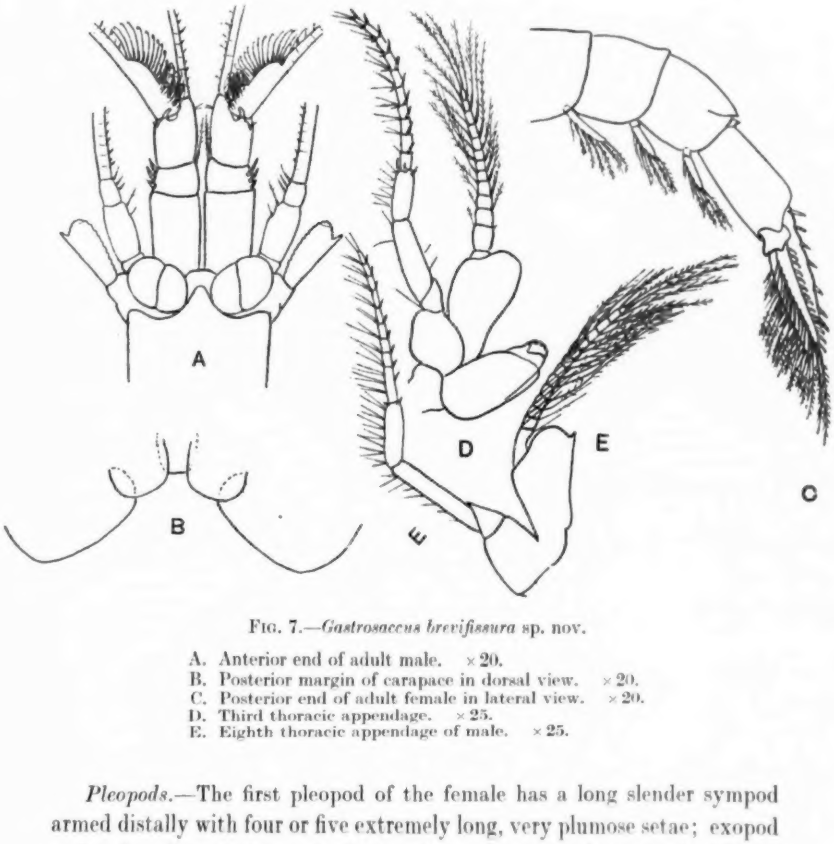

FIG. 7.—*Gastrosaccus brevifissura* sp. nov.

A. Anterior end of adult male. ×20.
B. Posterior margin of carapace in dorsal view. ×20.
C. Posterior end of adult female in lateral view. ×20.
D. Third thoracic appendage. ×25.
E. Eighth thoracic appendage of male. ×25.

Pleopods.—The first pleopod of the female has a long slender sympod armed distally with four or five extremely long, very plumose setae; exopod and endopod consisting each of a simple unsegmented plate armed with one or two long setae as shown in fig. 8, A. Remaining pleopods in the female rudimentary, in the form of simple unsegmented slender plates armed with a few long, plumose setae. *Pleopods of the male*: First pair with the sympod armed along its outer margin with nine to ten long, very plumose setae; exopod normal, composed of nine segments; endopod small, unsegmented, armed on each margin with two small plumose setae and distally with two very long plumose setae (fig. 8, B). *Second pair* biramous; exopod of nine

segments, stouter and twice as long as the seven-segmented endopod (fig. 8, C). *Third pair* with four-segmented exopod; first segment longer and twice as broad as the second, third and fourth segments subequal and longer than the second, fourth segment armed on its outer margin with two short, stout

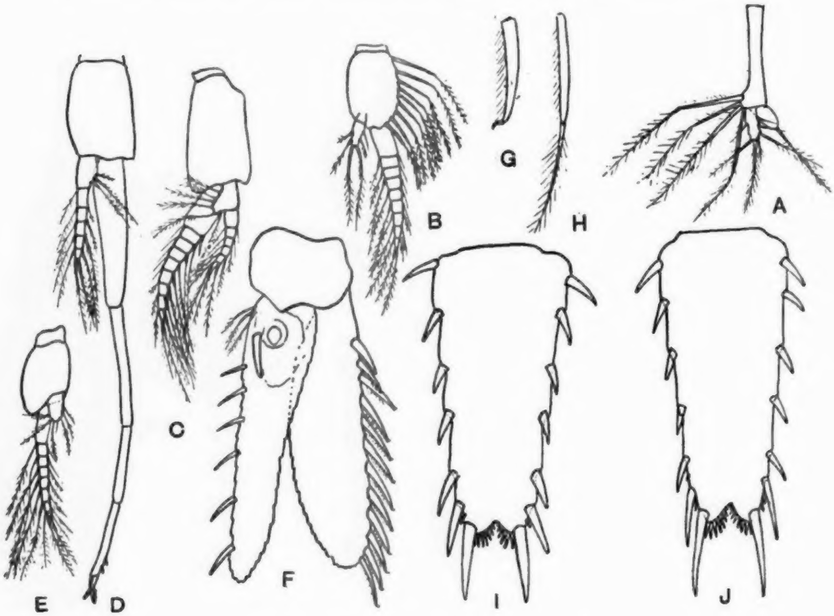

FIG. 8.—*Gastrosaccus brevifissura* sp. nov.

A. First pleopod of female. ×32·5.
B. First pleopod of male. ×32·5.
C. Second pleopod of male. ×32·5.
D. Third pleopod of male. ×32·5.
E. Fourth pleopod of male. ×32·5.
F. Uropod. ×45.
G. Spine from outer margin of exopod of uropod.
H. Seta from apex of exopod of uropod.
I. Telson of adult female. ×45.
J. Telson of adult male. ×45.

spines and terminating with two long, curved spiniform setae, one of which is barbed. The endopod is normal and composed of six segments (fig. 8, D). *Fourth and fifth pairs* with normal slender exopods; endopods each reduced to a single segment (fig. 8, E). *Uropod* only slightly longer than the telson; exopod broad, ovate, armed on its outer margin with twelve very strong spines which are very finely plumose on their posterior margins; endopod

very slightly longer than exopod, its inner margin unarmed for the proximal fifth of its length except for a group of three long fine setae at its base, the distal four-fifths armed with plumose setae and six long, slender, almost equally spaced spines. There is one very strong, posteriorly directed spine on the inner side of the statocyst. Each of the setae arming the uropods consists of two parts, a proximal portion which is thickened and plumose along its inner margin and precisely similar to the spines arming the outer margin of the exopod except that it is more slender, and a distal portion which is more slender and furnished all around with very long and very fine plumes. Towards the apex of the exopod the spines of the outer margin become more like the proximal portions of these setae, and each has a short curved tip which looks like the undeveloped distal portion, indicating that these spines are really modified setae (fig. 8, F, G, H).

Telson short and broad, lateral margins armed with seven very large strong spines; apical spines particularly long, more than one-fourth as long as the telson. In the space between the apical spine and the distal marginal spine there is one (rarely two) small spines, and in one specimen I found on one side a similar spinule in the next space (fig. 8, J). The *cleft* is very shallow, so that in some specimens it is little more than an emargination, armed with eight to nine graduated teeth on each side (fig. 8, I–J).

Length of adult male 11·5 mm.; of adult female 12 mm.

Remarks.—This species can be recognised by the rectangular posteriorly directed flaps on the posterior margin of the carapace, by the swollen appearance in lateral view of the fifth abdominal somite and the spinous projection from its posterior margin, by the well-developed endopod of the third male pleopod, and, particularly, by the shape and armature of the telson, with its extremely shallow cleft and the indications of a serial arrangement of the lateral spines shown by the presence of one or more small spinules between the apical and the distal marginal spines.

There is some diversity in the number of small spines in the space between the apical spine and the distal marginal one. All the specimens I examined had one such small spine, some had two on one side and one on the other, and some had two on each side. This diversity was not correlated in any way with the size of the specimens.

The genus *Gastrosaccus* now contains no fewer than twenty-one species and, although the differences which separate them are sufficiently distinctive to enable workers to distinguish one from another, it is not easy to give clear definitions whereby isolated individuals may be recognised. Unfortunately, in a number of cases the only conclusive evidence to be found is in the form of the pleopods of the male. Workers in the past have divided the genus into two groups based on the form of the endopod of the third pleopod of the male. In the one known as the *spinifer* group, this

endopod is of the normal, multiarticulate type as in *G. spinifer*, and in the other, the *normani* group, it is reduced to a single segment as in *G. normani*, or fused with the sympod and either completely lacking or represented by a small lobe.

In order to help workers to identify the species of this difficult genus, I have drawn up a key using, as far as possible, characters which are common to both sexes. Unfortunately it is impossible to do this entirely, since it is in the form of the male pleopods that some of the species have been separated. I have therefore given a synopsis of its salient characters under each species.

Key to the species of the genus GASTROSACCUS.

1. Lateral spines of telson in series of large spines with smaller ones in the spaces between them . . . . 2.
   Lateral spines of telson not in series . . . . 3.

2. Posterior margin of carapace entire. *Spinifer* group. Fourteen spines on inner margin of endopod of uropod. Telson cleft to one-eighth of its length; less than three times as long as broad . . . . *G. kempi* Tattersall 1922.
   Posterior margin of carapace with two very small lobes. *Spinifer* group. Thirteen spines on inner margin of endopod of uropod and two strong, backwardly directed spines on the statocyst. Telson cleft to one-sixth of its length. More than three times as long as broad . . *G. gordonae* sp. nov.

3. Posterior margin of carapace produced into a number of fine filaments or into a pair of lappets or lobes . . . . 4.
   Posterior margin of carapace entire . . . . 10.

4. Posterior margin of carapace armed with a fringe of filaments . . . . 5.
   Posterior margin of carapace armed with lappets or lobes . . . . . 7.

5. Posterior margin of fifth abdominal somite produced into a median spiniform process . . . . 6.
   Posterior margin of fifth abdominal somite not produced in the median line. Apex of scale shorter than spine terminating outer margin. *Spinifer* group; exopod of third pleopod of male very modified. Four spines on inner margin of endopod of uropod. Fourteen lateral spines on telson; telson cleft to one-sixth of its length . . . . *G. muticus* Tattersall 1915.

6. Posterior margin of fifth abdominal somite produced into a very definite spiniform process. Nine to ten spines on endopod of uropod. Six to eight lateral spines on telson . . . . *G. spinifer* (Goës) 1864.
   Posterior margin of fifth abdominal somite with definite spiniform process in young but not in adult. *Spinifer* group. Four spines on endopod of uropod. Eight to ten lateral spines on telson. Posterior margin of carapace with six to eight filaments . . . .*G. simulans* Tattersall 1915.

7. Posterior margin of carapace armed with reflexed lappets . . . . . 8.
   Posterior margin of carapace armed with large rectangular lobes, not reflexed . 9.

8. Posterior margin of carapace produced into a pair of oval lappets (one on either side of the median line) which are reflexed forwards. *Spinifer* group; both rami of second male pleopods well developed and straight. Six spines on inner margin of endopod of uropod. Six lateral spines on telson. *G. sanctus* (van Beneden) 1861.

Posterior margin of carapace armed with two extremely long, reflexed lappets which are truncate distally. *Normani* group; endopods of third pleopods of male completely lacking. Many spines on inner margin of endopod of uropod. Ten to twelve lateral spines on telson with wide space between penultimate and apical ones . . . . *G. dunckeri* Zimmer 1915.

9. Posterior margin of carapace produced into a median triangular lobe between the large rectangular lobes. *Normani* group; exopods of third pleopods of male very complicated. Two spines on endopod of uropod. Nine lateral spines on telson, the penultimate longer than the apical ones. *G. johnsoni* Tattersall 1936.

Posterior margin of carapace transverse between the large rectangular lobes. *Spinifer* group. Seven spines on inner margin of endopod of uropod. Seven lateral spines on telson, with one (rarely two) spines between penultimate and apical spines; cleft very shallow. Fifth abdominal somite produced into a small spiniform process . . . . *G. brevifissura* sp. nov.

10. Posterior margin of fifth abdominal somite produced in medial line into a linguiform process . . . . 11.

Posterior margin of fifth abdominal somite not produced . . . . . 12.

11. Posterior margin of fifth abdominal somite with a very short median process. Apex of antennal scale shorter than thorn terminating outer margin. *Spinifer* group. Six spines on inner margin of endopod of uropod; endopod longer than exopod. Six large lateral spines on telson, the penultimate and apical spines closely approximated . . . . *G. australis* Tattersall 1923.

Posterior margin of fifth abdominal somite produced into a very long process. Apex of scale equal in length to the thorn terminating the outer margin. *Normani* group. Six spines on inner margin of endopod of uropod. Nine lateral spines on telson, the penultimate and apical spines very long and closely approximated; remaining seven widely spaced and very small. *G. dissimilis*, Coifmann 1937.

12. *Spinifer* group . . . . 13.

Normani group . . . . 14.

13. Anterior margin of carapace with a narrow pointed rostrum and well-marked "shoulders." Ten spines on inner margin of endopod of uropod. Fourteen lateral spines on telson, apical spines very long and strong. *G. kojimaensis* Nakazawa 1910.

Anterior margin of carapace with obtusely pointed rostrum. Endopod of third pleopod of male two-segmented. Five to six spines on inner margin of endopod of uropod. Seven to eight lateral spines on telson. *G. vulgaris* Nakazawa 1910.

14. Second pleopods of male with normal exopods of six to seven segments; endopods reduced to a single segment; fourth and fifth pairs each with both rami reduced to a single segment . . . . 15.

Second pair of pleopods of male with both rami normal and multiarticulate; fourth and fifth pairs varied . . . . 16.

Endopod of third pleopods in the male reduced to an *outwardly* directed lobe; exopod composed of three segments terminating in two spines and a sinuous lash-like seta. Four spines on inner margin of endopod of uropod. Twelve lateral spines on telson (the penultimate much longer than the apical ones).
15 *G. pacificus* Hansen 1912.

Endopod of third pleopods in the male reduced to an *inwardly* directed lobe; exopod of four segments terminating in two small, simple spines. Five spines on inner margin of endopod of uropod. Ten lateral spines on telson, the penultimate and apical spines equal . . . . *G. indicus* Hansen 1910.

Endopod of third pleopod of male reduced to a small lobe. Fourth and fifth
16 pairs with both rami reduced to a single segment . . . . 17.

Fourth and fifth pairs of pleopods in the male with normal exopods of three to four segments; endopods each reduced to a single segment . . . . 18.

Rostrum very short, acutely pointed. Second pair of pleopods in the male with nine-segmented exopod half as long again as the seven-segmented endopod. Exopod of third pair seven-segmented. Four spines on inner margin of endopod of uropod. Eight lateral spines on telson . *G. pusillus* Coifmann 1936.

17 Triangular rostrum produced to distal end of first segment of antennular peduncle. Second pleopods in the male with five-segmented exopod and six-segmented endopod. Endopod of third pleopod absent. Four spines on endopod of uropod. Eight lateral spines on telson, penultimate and apical spines very long, the penultimate one the longer . *G. parvus* Hansen 1910.

Second pleopod of male with nine-segmented exopod and six-segmented
18 endopod . . . . 19.

Second pleopod of male with five-segmented exopod and four-segmented endopod. Exopod of third pleopod three-segmented . . . . . 21.

Endopod of second pleopod in the male markedly sigmoid. Seven spines on inner margin of endopod of uropod. Nine lateral spines on telson. (Lappets similar to those found in *G. sanctus* occur rarely on the posterior margin of the
19 carapace) . . . . *G. normani* G. O. Sars 1877.

Endopod of second pleopod of male straight. Exopod of third pleopod three to four-segmented . . . . 20.

Exopod of first pleopod of male six-segmented; of third, four-segmented; of fourth and fifth, three-segmented. Exopod of third pleopod ending in a minute claw, the penultimate segment expanded into a plate. Thirteen lateral spines on telson . . . . . . *G. bengalensis* Hansen 1910.

20 Exopod of first pleopod of male nine-segmented; of third, three-segmented; of fourth and fifth, four- and five-segmented respectively. Six spines on endopod of uropod. Seven widely spaced lateral spines on telson.
G. dakini Tattersall 1940.

Exopod and endopod of second pleopod in the male subequal. Exopod of third terminating in two equal spines, one of which is forked. Five spines on inner margin of endopod of uropod. Nine lateral spines on telson.
21 *G. erythraeus* Kossmann 1880.

Second pleopod of male with endopod shorter than exopod. Exopod of third pleopod terminating in three unequal spines which form a kind of talon. One spine on outer margin of second segment of antennular peduncle.
G. parerythraeus Nouvel 1944.

Sub-family **Mysinae.**

Tribe LEPTOMYSINI.

Genus *Leptomysis* G. O. Sars 1869.

Leptomysis tattersalli sp. nov.

(Fig. 9, A–G.)

Localities.—

Station No. 29: One adult male (8 mm.), 1 adult female (8 mm.). TYPES. Station No. 37A: One non-breeding female (immature). Station No. 38: One adult female. Station No. 41: One adult male, 11 adult females with eggs or advanced embryos in brood sacs, 12 juv.

Description.—Integument smooth. *Carapace* produced anteriorly into a very short triangular rostrum which barely covers the bases of the eye-stalks (fig. 9, D). *Antennular peduncle* short and more robust than in other species of the genus; first segment longer than the second and third together, its distal outer corner produced and armed with a group of long setae (fig. 9, A). *Antenna* with peduncle very slender. *Scale* short, lanceolate, setose all round; more than three times as long as broad at its widest part; apex rounded, distal portion bearing six setae cut off by a suture. The scale is only about half as long again as the antennular peduncle and is shorter and broader thân in any other species of the genus. Strong spine on outer distal corner of sympod (fig. 9, B, D). *Thoracic endopods* with fused carpus and propodus subdivided by transverse articulations into three sub-segments of which the first is the longest; dactylus very small and bearing a very fine bristle-like nail. *Pleopods of the male* well developed, multiarticulate and biramous; *fourth pair* with the exopod composed of seven segments; armed at the tip with one very long, strong spinous seta and one very small simple seta; endopod composed of eight segments, slightly shorter than the exopod; basal segment bearing a well-developed, long pseudobranchial lobe (fig. 9, E, F). *Uropod* with the exopod broad, half as long again as the telson; endopod only slightly longer than the telson; armed with a very close, regular, graduated row of spines from a point level with the middle of the statocyst to within a third of the length from the apex. These spines arise on the ventral surface a little way in from the margin and thus are longer than they appear in dorsal view. They are very small proximally but increase regularly in size towards the distal end of the row (fig. 9, G). *Telson* small and linguiform except for the pointed apex; nearly twice as long as broad at its base; lateral margins concave in the proximal third of their length, nearly parallel for the next third and then narrowing to a pointed apex; armed throughout with thirty to thirty-one

spines on each side; spines regular, with no signs of being grouped in series of larger spines with smaller ones between; more crowded at distal end of telson and somewhat larger than the more proximal ones; apex armed

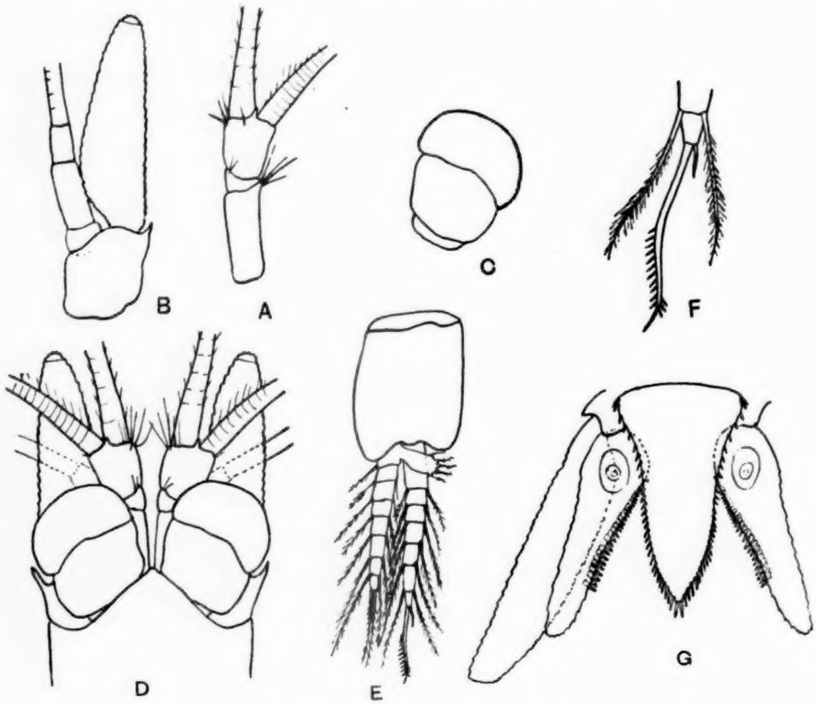

FIG. 9.—*Leptomysis tattersalli* sp. nov.

A. Antennule of female. × 32·5.
B. Antenna. × 32·5.
C. Eye. × 32·5.
D. Anterior end of female. × 32·5.
E. Fourth pleopod of male. × 32·5.
F. Distal end of exopod of fourth pleopod of male. Enlarged.
G. Posterior end. × 32·5.

with two larger spines which are one-thirteenth of the total length of the telson. I can see no trace of any small median spinules (fig. 9, G).

Length of adults of both sexes, 8 mm.

Remarks.—This species can at once be distinguished from other species of the genus by the short, broad, oval antennal scale with its rounded apex; by the form of the terminal setae of the exopod of the fourth pleopod of the

male; by the broad uropods and the arrangement of the spines arming the inner margin of their endopods and by the shape and armature of the telson. In all other species of the genus except *L. xenops* Tattersall (1922, p. 470) and *L. australiensis* Tattersall (1927, p. 246) the spines arming the telson are arranged in more or less well-defined series of larger ones with smaller ones in the spaces between them. In *L. xenops* the spines are arranged in a regularly graduated row, but the apex is truncate and armed with four very large, powerful spines and a pair of median spinules. The telson in *L. australiensis* is more like that of my species but has the apex broadly rounded. That species can readily be distinguished from *L. tattersalli* by the shape of the antennal scale, which is very long and slender with a pointed apex, and by the difference in the modification of the setae of the fourth pleopod of the male.

Genus *Tenagomysis* G. M. Thomson 1900.

This genus was established by G. M. Thomson (1900, pp. 482–86) for specimens from Brighton, near Dunedin, New Zealand, and the genotype *Tenagomysis novae-zealandiae* remained for some years the only representative of the genus. Tattersall (1918, p. 10) added a second species, *T. tenuipes,* which he instituted for a specimen from Carnley Harbour, Auckland Islands. This species showed certain features which necessitated some modification of the existing definition of the genus. Tattersall, therefore, re-defined the genus and discussed its position in the sub-family Mysinae. Tattersall (1923, pp. 273–304) published a report on the material collected by the "Terra Nova" during 1911–12. He described no fewer than six new species from this material and a seventh from specimens collected by Professor Chilton at Parakai, New Zealand. The genus then contained nine species, all of which came from the South Pacific. Tattersall fully discussed the genus and drew up a very clear key for the identification of its species. Since then only two further species have been added to the genus, *T. orientalis* Ii (1937, p. 196) for specimens from Azino, Japan, and *T. atlantica* Nouvel (1942, p. 10) for specimens from the Gulf of Gascony, Bay of Biscay.

Until now all the representatives of the genus but one have come from the Pacific. It is, therefore, with great interest that I am able to record a specimen from Richard's Bay, Natal, which undoubtedly belongs to this genus. The single specimen is a male, which, I think, is adult, measuring 6 mm. It is, unfortunately, damaged, having one antennule, nearly all the thoracic endopods and both of the fourth pleopods missing.

Tenagomysis natalensis sp. nov.

(Fig. 10, A–C.)

Occurrence.—Station No. 14. One male (6 mm.). Collected by Mr. A. D. Harrison.

Description.—*General form* small and slender. *Carapace* short; produced anteriorly into an acutely pointed rostrum which extends beyond the

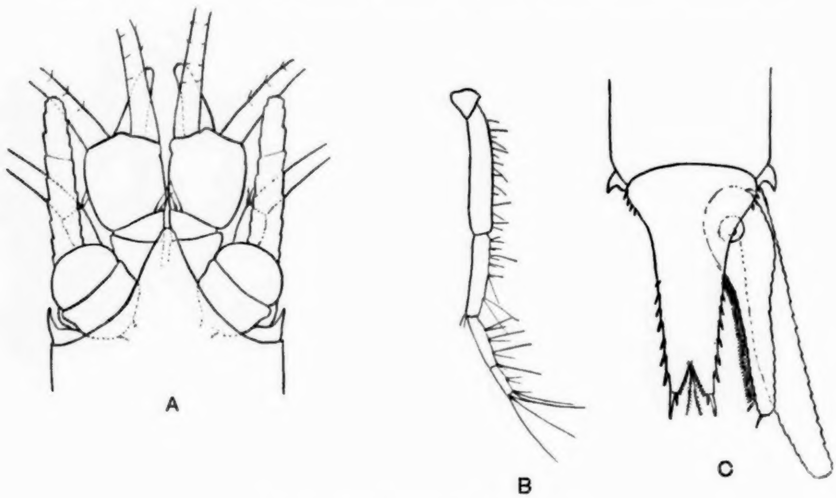

Fig. 10.—*Tenagomysis natalensis* sp. nov.

A. Anterior end of male. ×45.
B. Third thoracic endopod. ×45.
C. Posterior end. ×45.

eyes to half-way along the second segment of the antennular peduncle; antero-lateral angles rounded; posterior margin emarginate, leaving the last two thoracic somites exposed (fig. 10, A). Sixth abdominal somite one-third as long again as the fifth. *Antennule* short and very robust; first and third segments subequal in length; second segment very short; third segment nearly square in dorsal view; large male lobe present but in this specimen it is not very densely covered with hairs. This may be a sign of immaturity or they may have been broken off (fig. 10, A). *Antennal scale* small; narrowly linear; seven times as long as broad; setose all round; extending beyond the distal end of the antennular peduncle by about one-fourth of its length; apex bluntly rounded; distal suture present,

cutting off rather more than one-fourth of the scale; *peduncle* small and slender; about half as long as the scale; very strong spine present at the outer distal corner of the sympod (fig. 10, A). *Eyes* robust and short; set deeply so that the cornea barely projects laterally beyond the lateral margins of the carapace; length and breadth subequal; cornea large, occupying about one-half of the total organ; no ocular papilla; colour in preserved specimen golden brown (fig. 10, A). *Thoracic limbs*: As far as can be made out without dissection, the first and second thoracic limbs are similar to those figured by Ii (1937, p. 199, fig. 22) for *T. orientalis*. Of the other thoracic appendages only one of the third pair possessed an endopod, and there was an endopod loose in the tube with the specimen. *Third thoracic appendage* with the endopod slender and delicate; tarsus composed of three segments, the carpus, a shorter, unsegmented propodus, and a very small dactylus armed terminally with a single, long, very slender seta (fig. 10, B). The large basal segments of the exopods are without spines at the outer distal angle. *Genital organ* of eighth thoracic appendage of the male, large, ampulla-shaped, equal in length to the basal segment of the exopod. *Pleopods of the male*: First pair with the endopod short and unsegmented; exopod multiarticulate; second and third pairs well developed, biramous and multiarticulate. Fourth pair missing. Fifth pair similar to the second and third pairs but smaller. *Uropod* with the endopod slightly longer than the telson; inner margin armed with a very close row of about fifty spines, extending from near the statocyst almost to the apex. These spines are very regular, but become gradually larger towards the distal end of the margin, and the row terminates in a distinctly larger spine; single strong spine present on inner margin of the apex. Exopod one-third as long again as the endopod (fig. 10, C). *Telson* equal in length to the sixth abdominal somite; not quite twice as long as broad at its base; lateral margins rounded at the base, converging and concave in the proximal third of their length, thence converging very slightly to the apical lobes; armed with four small spines at the base and a graduated row of eight spines on the distal half of each margin; terminal spine measuring one-eighth of total length of telson and flanked on its inner side by a small spine of less than half its length. *Cleft* with widely open, straight sides armed with about fifteen close-set teeth on each side and a pair of long, median, plumose setae (fig. 10, C).

Length.—6 mm.

Remarks.—In the absence of the fourth pleopod it is not possible to say definitely if the specimen is fully adult. The male lobe of the antennule is large but is not densely hirsute. The genital organ of the eighth thoracic appendage is large and well developed.

This species may be distinguished from others of the genus by the long,

triangular rostrum with its narrow rounded apex; the short, robust antennules; the length and proportions of the antennal scale; the robust, deeply set eyes; the slender endopods of the thoracic appendages with the tarsus consisting of three simple, undivided segments; the arrangement of the spines arming the inner margin of the endopod of the uropod and the shape and armature of the telson. In all the other species of the genus the lateral margins of the telson are armed throughout with spines, usually small and not arranged in series. In *T. natalensis* only the distal half of the lateral margins is armed with spines in addition to the few spines at the proximal end. If this specimen is not fully adult, this feature may be a sign of immaturity, and older individuals may show no unarmed portion in the lateral margins.

Distribution.—This is the first time that a species of *Tenagomysis* has been found outside the Pacific Ocean except for *T. atlantica* Nouvel from the Bay of Biscay. It is to be hoped that further exploration of South African waters may yield other specimens of this interesting species so that the female may be described and the fourth pleopod of the male may be studied.

Tribe MYSINI.

Genus *Mesopodopsis* Czerniavsky.

Mesopodopsis africana sp. nov.

(Figs. 11, A–C; 12, A–L.)

Localities.—

Station No. 1: Seven males; 8 females. Station No. 2: Twenty adult males, 4 juv.; 68 adult females (breeding), 24 juv. Station No. 4: Thirty-four adult males, 17 juv.; 31 adult females (breeding), 15 juv. Station No. 5: One adult male; 2 breeding females (colour very dark, nearly black). Station No. 6: About 40 adult males and 60 females. This material is in bad condition and most of the specimens are incomplete. Station No. 7: One male; 1 female. Station No. 8: Many adults and juveniles of both sexes. TYPES. Station No. 9: Seven breeding females, 2 juv. Station No. 10: One adult male; 4 adult females. Station No. 14: Fifty-four breeding females and 7 non-breeding; 18 males, 6 juv. Station No. 15: One juv. Station No. 16: Two hundred to three hundred, nearly all juvenile with a few adults of both sexes. Station No. 17: One adult ovigerous female. Station No. 18: Two fragments. Station No. 31: One ovigerous female.

Description.—*General form* long and slender, particularly in the thoracic region. *Carapace* very short, leaving the whole of the last three thoracic somites exposed; anterior end produced into a broad, obtusely pointed rostral plate which does not cover any part of the eyes; antero-lateral angles produced into long acute processes (figs. 11, A–B). *Abdomen* comparatively robust, first somite short, second to fifth somites subequal, sixth

nearly twice as long as the fifth (fig. 11, A). *Antennule*: First segment longer than second and third segments together; outer distal corner armed with one very strong, plumose seta and a small group of smaller ones; third segment armed at about the middle point of its inner margin with a single very long strong plumose seta, and on its inner distal corner with a group of three or four similar ones. In the male there is, as in other members of the

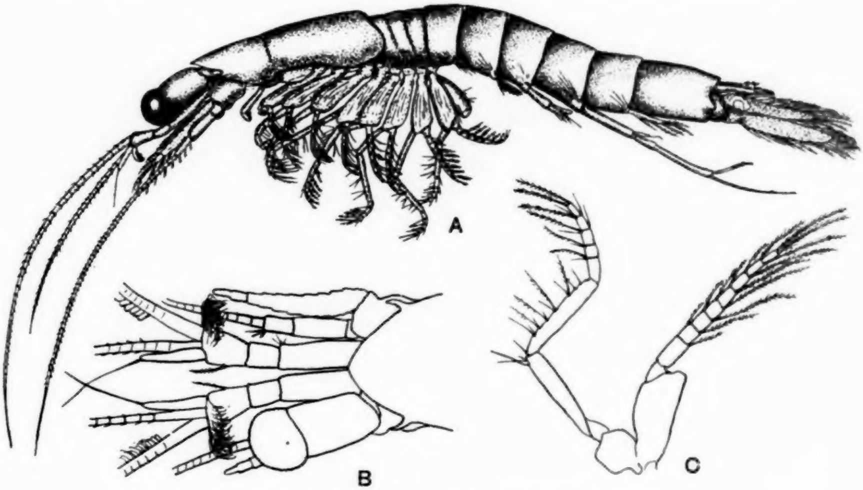

FIG. 11.—*Mesopodopsis africana* sp. nov.

A. Adult male in lateral view. × 20.
B. Anterior end of male. × 35.
C. Fourth thoracic appendage. × 42·5.

genus, in addition to the long, well-developed hirsute lobe, a fourth appendage consisting of a long, slender, conical outgrowth tipped with a single very long seta (figs. 11, B; 12, A). Though showing almost the same relative proportions to one another as they do in the well-known *Mesopodopsis slabberi* (P. J. van Beneden), the antennule, antenna and eye are all much shorter and more robust than in that species, so that the animal appears much less attenuated at its anterior end. *Antennal scale* similar in shape to that of *M. slabberi* but shorter; extending almost to the distal end of the antennular peduncle; small distal suture present; *peduncle* slender, about two-thirds of the length of the scale (figs. 11, B; 12 B). *Eye* large and robust; not quite twice as long as broad; shorter and broader than in either of the other two species of the genus; extending forward slightly beyond the distal margin of the second segment of the antennular

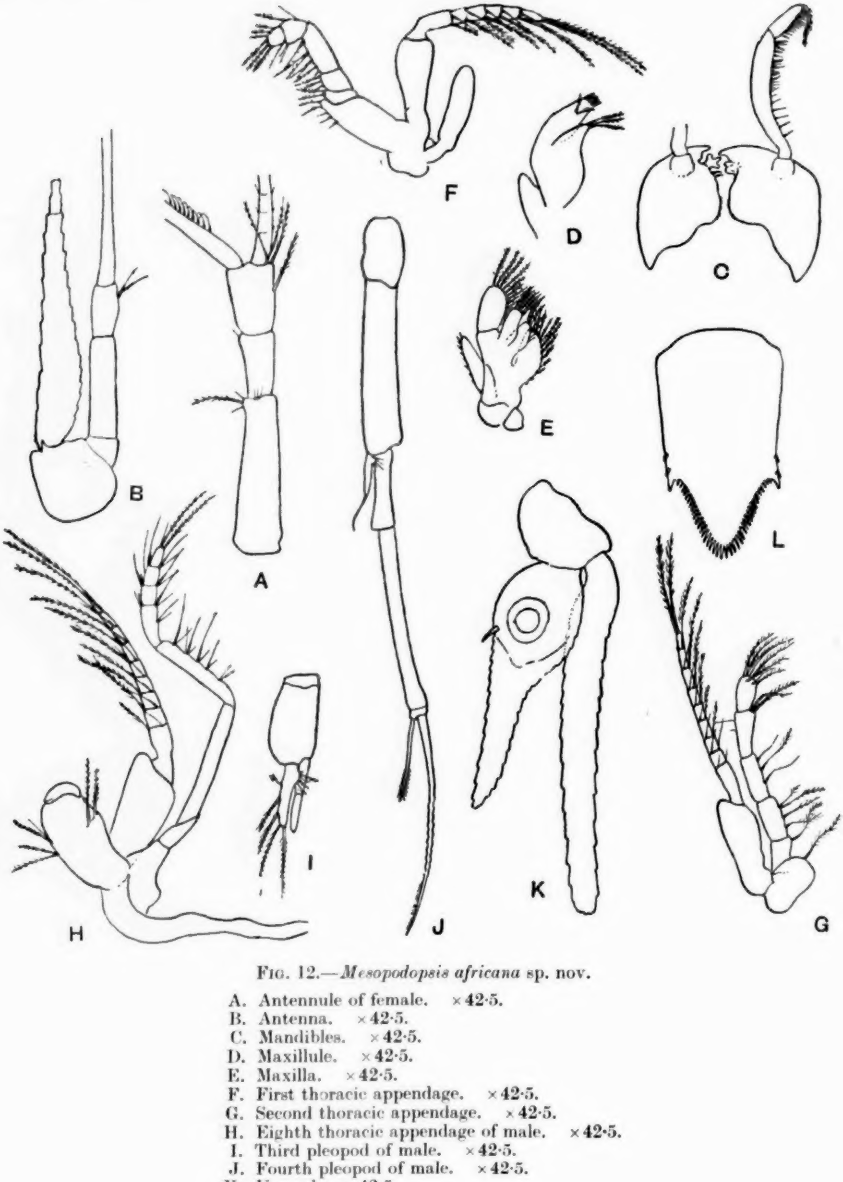

FIG. 12.—*Mesopodopsis africana* sp. nov.

A. Antennule of female. ×42·5.
B. Antenna. ×42·5.
C. Mandibles. ×42·5.
D. Maxillule. ×42·5.
E. Maxilla. ×42·5.
F. First thoracic appendage. ×42·5.
G. Second thoracic appendage. ×42·5.
H. Eighth thoracic appendage of male. ×42·5.
I. Third pleopod of male. ×42·5.
J. Fourth pleopod of male. ×42·5.
K. Uropod. ×42·5.
L. Telson. ×52·5.

peduncle (fig. 11, A, B). *Mandibles, maxillule* and *maxilla* as shown in figures 12 C–E. These appendages show very little difference from those figured by G. O. Sars for *M. slabberi* (1877, pl. 12, figs. 3, 4, 6 and 7). *First and second thoracic appendages* small and slender and of the usual Mysid type (figs. 12, F–G). *Third to the seventh thoracic appendages* very slender and delicate; endopods with only five segments distal to the "knee" and no nail (fig. 11, G). *Eighth thoracic appendage* somewhat more robust than the preceding appendages, and longer; endopod with only four segments in the tarsus. The male genital appendage is very large and is obscurely two-lobed at its distal end (fig. 12, H). *Third pleopod of the male* biramous, endopod unsegmented, with a feebly developed pseudobranchial lobe on the outer margin at its base; exopod slightly longer than endopod and more slender; divided by a transverse articulation into two equal segments, unadorned with setae (fig. 12, I). *Fourth pleopod of the male* very similar to that of *M. slabberi*; endopod extremely small and short; only half as long as the first segment of the exopod; composed of a single segment with a feebly developed pseudobranchial lobe at its base; *exopod* very long, extending backward well beyond the proximal end of the telson; composed of three segments, the second of which is twice as long as the first, third segment very short and armed with one very long and one shorter seta. The larger seta is more than twice as long as the shorter and its margins are curiously wavy in outline in the middle region of its length; distally it is finely plumose. The smaller, inner seta is spinous (fig. 12, J). *Uropod* shorter than in the other species of the genus; exopod linear and slender; endopod wide proximally with a very large statocyst and narrowing distally; strong spine present on the inner margin at the side of the statocyst (fig. 12, K). *Telson*: Lateral margins almost straight and parallel; only slightly longer than the width of the telson at its base; armed distally with three small spines at each side, the terminal one being mounted on a tooth-like projection and thus appearing larger than the other two. Apex produced considerably as a broad tongue with its margin armed all round with a very close row of teeth or serrations which are larger at the distal end; apical projection slightly less than one-third of the total length of telson. The telson is hollowed from above into a trowel shape (fig. 12, L).

Length.—Adults of both sexes 4·6 mm.

Colour.—The colour is given as "red when alive" on one of the tubes, but there is evidently some variation in colour, for the specimens from Station No. 5 are very dark, almost black.

Remarks.—Up to the present only two species have been referred to the genus *Mesopodopsis*: *M. slabberi* (P. J. van Beneden), 1861, p. 18, and *M. orientalis* (Tattersall), 1908, p. 236. In many respects this new species from South Africa is intermediate between them, possessing some characters

of the one and some of the other. It resembles *M. slabberi* in the shape of the rostrum and the form of the fourth pleopod of the male and the uropods, but it can at once be distinguished from it by the much shorter, thicker eyes and the shorter antennules and antennae, the longer apex of the telson and the fewer spines arming its lateral margins.

It resembles *M. orientalis* in the length of the antennules, antennae and eyes, and in the form of the telson, but differs from it in the shape of the rostrum (this is rounded and not produced forward in *M. orientalis*), the broader scale, the thicker eyes, the form of the fourth pleopod of the male and by the presence of a strong spine on the inner margin of the endopod of the uropod. In *M. orientalis* the first segment of the exopod of the fourth pleopod of the male is very short, only half the length of the small endopod (Tattersall, 1908, pl. xxii, fig. 9), while in both *M. slabberi* and *M. africana* the reverse is the case.

M. africana may be distinguished by the fewer segments in the tarsus of the thoracic endopods, having only five in the third to the seventh thoracic appendages and only four (rarely five) in the eighth. In *M. slabberi* there are from seven to eight segments, and in *M. orientalis* from five to nine segments, in the tarsus of these appendages. Another useful point of difference is shown in the form of the third pleopod of the male (fig. 12, I). In both the other species the exopod is much shorter and more slender than the endopod, but in *M. africana* the exopod is slightly longer than the endopod and almost as broad.

At most of the stations from which *M. africana* was taken quite considerable numbers were captured, and it would appear that it resembles the other two species of the genus in being a gregarious form, living in large swarms at, or very close to, the bottom.

Mesopodopsis slabberi (P. J. van Beneden) 1861.

1778. Slabber, M., "Steurgernaal met trompetswyze oogen," Natuurkundige Verlustigingen, p. 136, pl. 15, fig. 3.

1861. van Beneden, P. J., Récherches sur la faune litt. de Belgique. Crustacés, p. 18, pl. 6.

1863. *Mysis slabberi* Goës, Crust. decap. podoph. mar. Sueciae . . . p. 16.

1876. *Macropsis slabberi* G. O. Sars, "Middelhavets Mysider," Arch. Math. Naturv., , p. 28, pls. XI–XIII.

1882. *Mesopodopsis slabberi* Czerniavsky, Monog. Mysid. Imp. Ross., **1**, p. 145.

Localities.—

Station No. 20: More than 100, mainly breeding. Station No. 21: One male; 1 adult female and some fragments. Station No. 22: Thirteen

males, 20 juv.; 7 females with eggs, 14 females with empty brood sacs, 24 juv. females. Station No. 23: One adult female non-breeding. Station No. 24: Many hundreds, both adults and juv., of both sexes. Station No. 27: Seven adult males, 3 juv.; 10 adult females, 6 juv. Station No. 28: Hundreds of both sexes, nearly all juv.

Remarks.—This species has been recorded from S.W. Africa by Zimmer in 1912 and from the Cameroons by Tattersall (1927, p. 316). It is found all round the coasts of Europe and throughout the Mediterranean, living in shallow waters in great swarms. From the numbers taken at some of the stations in the present collection it is evident that it is also living in dense swarms in S. African coastal waters. I can find no record of it from the eastern waters of South Africa.

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A NEW SPECIES OF THE CRINOID GENUS *CYCLOMETRA* FROM SOUTH AFRICA.

By Austin H. Clark.

WITH REMARKS AND ADDITIONAL NOTES ON THE GENOTYPE.

By Ailsa M. Clark.

(With Plates XV and XVI and one Text-figure.)

Family ANTEDONIDAE.

Sub-family Zenometrinae.

Cyclometra multicirra sp. n.

AFR 759. 30° 15′ S.; 14° 5′ E. (west coast of Cape Province). 461 metres. 1 specimen.

Description.—The centrodorsal is conical with slightly convex sides, 3·3 mm. broad at the base and 4 mm. high, with the proximal border straight. The cirrus sockets are closely crowded all around the centrodorsal without division into radial groups, and are arranged in three columns of four or five each under each radial; the two lateral columns under each radial are straight and regular, but the median column has at the proximal end one or two sockets between it and a lateral column.

The cirri are LXXX, the longest peripheral 40 mm. long, with 31 segments of which the first three are broader than long, the fourth is half as long again as broad, and those following increase in length to the eighth or tenth which is from two and a half to three times as long as broad or even somewhat longer. The distal half of the cirri taper slightly to a rather delicate tip. The length of the segments in the distal half slowly decreases so that the last five or six are only slightly, or not at all, longer than broad. The longer earlier segments have slightly flaring ends which overlap the bases of those succeeding. The distal segments increase slightly in width from the proximal to the distal end, the dorsal profile being almost straight and continuous with the profile of the preceding and succeeding segments, the ventral profile forming an angle at the distal end where it extends below the base of the following segment. The short distal segments are rather sharply carinate dorsally. The penultimate segment is slightly longer than

broad; the opposing spine is represented by a broad blunt tubercle. The terminal claw is about as long as the penultimate segment, rather slender and slightly curved.

The cirri decrease in length from the peripheral to the apical, the latter (all broken) being apparently scarcely half the length of the former.

The ends of the basal rays are visible as very small rounded-triangular tubercles in the interradial angles.

The radials are very short, with the distal border rather strongly concave so that the anterolateral angles extend well up into the interradial areas where they separate entirely the bases of the IBr_1. The distal half is turned outward, especially in the lateral portions. The IBr_1 are short, about four times as broad as the median length, with the lateral edges slightly convergent and widely separated from those of their neighbours and the distal edge slightly concave, incised by the posterior projection of the axillary with which it forms an apically well-rounded synarthrial tubercle the sides of which in profile make an angle of about 120° with each other. The IBr_2 (axillaries) are about as long as broad, with the proximal sides nearly straight and making an angle of about 90° with each other and the distal strongly concave, so that the distal angle and the lateral angles, which extend well beyond the anterolateral angles of the IBr_1, are acute. The edges of the elements of the IBr series are smooth, the two distal edges of the axillaries slightly everted.

The 10 arms are probably a little more than 100 mm. long. The first brachials are short, about three times as long exteriorly as interiorly; the short interior sides of each pair make a straight line with each other. The second brachials are about half again as large as the first, approximately triangular, with the proximal angle incising the first and making with them a synarthrial tubercle which resembles that on the IBr series except that the apex is more sharply pointed.

The first syzygial pair (composed of brachials 3 + 4) is about half again as broad as long with, like the first and second brachials, slightly everted and finely spinous ends. The next four brachials are wedge-shaped, about twice as broad as the median length, with the longer side about twice as long as the shorter. Following the second syzygy, the brachials soon become more obliquely wedge-shaped, almost triangular, and nearly or quite as long as broad. The distal ends of the brachials are very finely spinous, but are not everted or produced. Distally the brachials become somewhat less obliquely wedge-shaped and longer.

Syzygies occur between brachials 3 + 4, 9 + 10, and 14 + 15, and distally at intervals of usually 3 muscular articulations.

P_1 is about 15 mm. long, slender, tapering rather more rapidly in the proximal than in the distal half and becoming very flexible in the distal

third, with 33–34 short segments of which the first five are broader than long and the remainder are slightly longer than broad. The first five or six have the dorsal side convex and finely spinous, and those following until near the tip are very slightly constricted centrally.

P_2 is similar to P_1 but stouter and slightly longer with 24–27 segments which distally are proportionately slightly longer than those of P_1.

P_3 is 10 mm. long with 17–19 segments, a little stouter than P_2 at the base but tapering more gradually and stiffened, without the flagellate tip of the two preceding pinnules. The segments become about twice as long as broad on the fifth, and three times as long as broad distally. The sixth–tenth segments bear a slender fusiform gonad.

The following pinnules are similar to P_3. P_8 is 12 mm. long with 22 segments, with a gonad on the fourth–ninth.

The distal pinnules are about 18 mm. long with about 27 segments most of which are about twice as long as broad, the outermost about three times as long as broad. The segments of the middle and distal pinnules have finely spinous distal ends.

The disk is naked.

The colour (in alcohol) is brownish white, the pinnules purplish, becoming distally purple with the articulations narrowly white.

Remarks (by Ailsa Clark).—In a letter to me Dr. Clark said: "This new species certainly belongs to the Zenometrinae, not to the Heliometrinae to which *Cyclometra flavescens* was referred." He suggested that I should re-examine the type of *C. flavescens*, particularly with regard to the centrodorsal, to ascertain whether it also should be referred to the Zenometrinae. I have done this and find that his suspicions are well founded, for the cirrus sockets are arranged in vertical columns on the centrodorsal, rather than in alternating rows. I append here a supplementary description of the type of *Cyclometra flavescens* A. H. Clark.

[*Cyclometra clio*, Dr. Clark tells me, is not a *Cyclometra* but should be referred to the Bathymetrinae.]

Cyclometra flavescens A. H. Clark.

(Text-fig. 1.)

Cyclometra flavescens A. H. Clark, 1911, p. 87.

Additional Observations on the Holotype.

Locality.—North-west of Sokotra, 14° 20′ N., 52° 30′ E. 1200 fathoms.

Centrodorsal rounded conical, 4 mm. wide at the base and 2·7 mm. high. The cirrus sockets are arranged in 15 vertical columns each of 2 or 3 sockets.

The proximal ring round the apex of the centrodorsal includes 10 sockets, so that two of these correspond to three columns of the other two rows and consequently alternate in position with them to some extent. However, the two other sockets in each column lie directly below one another.

There are XL cirri, not XXVIII as Dr. Clark states. The shorter distal segments are somewhat carinate dorsally, the edge appearing smoothly curved in lateral view. The opposing spine is quite conspicuous,

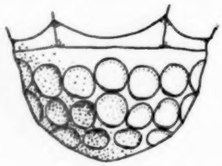

FIG. 1.—*Cyclometra flavescens.* Diagram of the centrodorsal, to show the arrangement of the cirrus sockets.

while the terminal claw is slightly curved and almost equals in length the penultimate segment.

The IBr_1 is rectangular, about three times as wide as long; it forms a conspicuous, rounded synarthrial tubercle with the IBr_2 (axillary). The latter is not quite as long as broad, being 3 mm. wide and only 2·5 mm. in length, the distal angle measures approximately 90°.

The first brachial is short and wedge-shaped, twice as long exteriorly as interiorly; it forms a synarthrial tubercle with the larger second brachial. The following brachials are more or less rectangular, with only a slight tendency to be wedge-shaped until after the second syzygy (9 + 10), where they assume a more triangular form. Distally the segments become increasingly long, almost twice as long as wide.

P_1 has about 42 segments and is 17 to 19 mm. long. The segments are not much longer than broad distally. However, P_2, which has about 32 segments and is 14 mm. long, has the distal ones more than twice as long as broad, and P_3, with 25 segments totalling 12 mm. in length, has distal segments three times as long as wide. P_4 and P_5 are progressively shorter, with more attenuated and longer distal segments. The distal pinnules have about 20 segments, each of which is 3–4 times as long as wide.

REFERENCE.

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Cyclometra multicirra sp. n. × 1.

Austin H. Clark. *Neill & Co. Ltd.*

SOME ECHINODERMS FROM SOUTH AFRICA.

By AILSA M. CLARK, Department of Zoology,
British Museum (Natural History).

(With Plate XVII and three Text-figures.)

The specimens which form the basis of this report were sent to the British Museum by Professor J. H. Day of the University of Cape Town and were collected during an ecological survey made by the University, chiefly in Table Bay and False Bay. Some material was also obtained by trawlers and by the survey vessel "Afrikana" in deeper waters to the north-west and south of Cape Town, besides a small collection from Knysna Lagoon. A single specimen is included from Durban Bay.

The South African Echinoderm fauna has been studied in some detail, particularly by H. L. Clark and by Mortensen. In his paper on the Asteroids and Ophiuroids he collected, the latter includes a synopsis of all the species known to occur between Natal and Luderitz Bay up to 1933. Thirty-two of the 85 Asteroid species mentioned in that list are included in the present collection and 15 out of the 82 Ophiuroids. Eight of the 9 Echinoids taken are mentioned in H. L. Clark's 1923 paper, the ninth, *Stereocidaris excavata* Mortensen (1932), is described in his "New Contributions to the Knowledge of the Cidarids". The three previously known Crinoids in this collection are all mentioned by H. L. Clark and also by Gislen in 1938. The new Crinoid species has been described by Dr. A. H. Clark and, together with some notes by myself, is the subject of a separate paper. Dr. Mortensen has very kindly helped me by confirming the identification of the *Stereocidaris excavata* specimen.

Nearly all the species found in the present collection are described, or references to them are given, in the papers mentioned above; consequently, to avoid repetition, many of them are not remarked on further than in the table (see p. 194).

Note.—Soundings are given both in fathoms and in metres in the table, for easier comparison with the depths given by others, but in metres alone in the text.

Species.	Locality.	Depth in Metres.	Depth in Fathoms.	Nature of Bottom.	No.	Stat. No.
Asteroidea.						
Luidiaster hirsutus Studer	45 miles N.W. of Cape Town.	329	180	..	2	TRA 14
	W. coast of S. Africa. 30° 02′ S. 15° 02′ E.	364	199	Green sand	1	AFR 743
	S. of the Cape. 35° 15′ S. 18° 39′ E.	547	299	..	1	AFR 831
Dipsacaster sladeni subsp. *capensis* subsp. n.	45 miles N.W. by N. of Cape Town.	357	195	..	1	TRA 12
	45 miles N.W. by N. of Cape Town.	329	180	..	1	TRA 13
Psilaster acuminatus Sladen	W. coast of S. Africa. 31° 14′ S. 16° 37′ E.	272	149	Polyzoa and rock	2	AFR 728
	W. coast of S. Africa. 32° 01′ S. 16° 36′ E.	364	199	Dark green mud	1	AFR 710
	S. of the Cape. 35° 15′ S. 18° 39′ E.	547	299	..	1	AFR 831
Astropecten irregularis var. *pontoporaeus* (Sladen)	False Bay, Fishoek Bay.	8	4½	Sand	2	FB 1058
	False Bay, Fishoek Bay. 34° 09′ S. 18° 27′ E.	17	9	Sand	3	FB 1065
	False Bay, off Fishoek Bay.	22	12	Sand	3	FB 1059

Astropecten irregularis var. *pontoporaeus* (Sladen)	False Bay. 34° 08′ S. 18° 29′ E.	23–27	13–15	Sand and broken shells	2	FB 1062
	W. coast of S. Africa. 30° 22′ S. 16° 50′ E.	185	101	Dark green sand	2	AFR 738
	Off Danger Point.	66	36	Rock	4	AFR 864
	Position not available.	. .	. .	. .	1	AFR 994
	Off Cape Infanta.	66	36	. .	2	TRA 25
Astropecten antares Döderlein	Knysna Lagoon.	2–6	1–3	Muddy sand	1	KNY 6
Luidia africana Sladen	Off Danger Point.	66	36	Rock	3 arms	AFR 864
	W. coast of S. Africa. 30° 02′ S. 15° 02′ E.	364	199	Green sand	1	AFR 743
Pseudarchaster tesselatus Sladen	48 miles W. by S. of Cape Town.	402	220	. .	1	TRA 7
	W. coast of S. Africa. 30° 42′ S. 15° 59′ E.	201	110	Light green sand	2	AFR 736
	45 miles N.W. by N. of Cape Town.	357	195	. .	1	TRA 12
Mediaster capensis H. L. Clark	34° 39′ S. 18° 42′ E.	168	93	Green mud	1	AFR 882
Ceramaster patagonicus var. *euryplax* H. L. Clark	W. coast of S. Africa. 31° 30′ S. 17° E.	366	200	. .	1	AFR 723–5–7
	48 miles W. by S. of Cape Town.	402	220	. .	1	TRA 7
	45 miles N.W. by N. of Cape Town.	329	180	. .	2	TRA 13

Species.	Locality.	Depth in Metres.	Depth in Fathoms.	Nature of Bottom.	No.	Stat. No.
Calliaster baccatus Sladen	Off Danger Point.	38	21	Rock	1	AFR 866
Toraster tuberculatus (Gray) (nom. nov. for *Tosia tuberculata*)	W. coast of S. Africa. 31° 30′ S. 17° E.	366	200	. .	1	AFR 723–5–7
	45 miles N.W. by N. of Cape Town.	329	180	. .	2	TRA 13
Hippasteria phrygiana var. *capensis* Mortensen	45 miles N.W. by N. of Cape Town.	329	180	. .	2	TRA 13
Hippasteria strongylactis H. L. Clark	45 miles N.W. of Cape Town.	375	205	. .	1	TRA 10
Odontaster australis H. L. Clark	W. coast of S. Africa. 31° 23′ S. 16° 30′ E.	366	200	Dark mud and rock	2	AFR 729
Tylaster meridionalis Mortensen	W. coast of S. Africa. 30° 07′ S. 15° 50′ E.	205	112	Sand and mud	1	AFR 762
Spoladaster brachyactis (H. L. Clark)	W. coast of S. Africa. 30° 07′ S. 15° 50′ E.	205	112	Sand and mud	1	AFR 762
Chondraster elattiosus H. L. Clark	48 miles W. by S. of Cape Town.	402	220	. .	1	TRA 7
Poraniopsis capensis H. L. Clark	W. coast of S. Africa. 29° 16′ S. 14° 48′ E.	238	130	Clay, sand and rock	1	AFR 775
Patiria bellula (Sladen)	Table Bay, off Blaauberg.	9	5	Sand and rock	1	TB 90
	False Bay, off Fishoek Bay.	15	8	Shell	2	FB 1060
	Off Danger Point.	37	20	Rock	1	AFR 865

Henricia ornata (Perrier)	False Bay. 34° 07′ S. 18° 31′ E.	27–28	15	Rock	1	FB 1053
Henricia abyssalis (Perrier)	45 miles N.W. by W. of Cape Town.	329	180	. .	1	TRA 9
	W. coast of S. Africa. 29° 13′ S. 14° 59′ E.	198	108	Mud, sand and rock	1	AFR 774
Henricia studeri (Perrier)	Position not available.	. .	. .	. .	1	AFR 791
Crossaster penicillatus Sladen	45 miles N.W. by N. of Cape Town.	357	195	. .	1	TRA 3
	45 miles N.W. by N. of Cape Town.	357	195	. .	1	TRA 11
	S.S.E. of Cape Agulhas. 36° 25′ S. 21° 08′ E.	177	97	Sand	1	AFR 945
Lophaster quadrispinus H. L. Clark	42 miles W. by N. of Cape Town.	329	180	. .	1	TRA 8
Pteraster capensis Gray	W. coast of S. Africa. 29° 31′ S. 15° 17′ E.	187	102	Sand and mud	1	AFR 765
	Position not available.	. .	. .	. .	1	AFR 791
	W. coast of S. Africa. 31° 14′ S. 16° 37′ E.	272	149	Polyzoa and rock	1	AFR 728
Pteraster gibber Sladen	W. coast of S. Africa. 32° 38′ S. 16° 52′ E.	347	190	Clay and sand	1	AFR 691
Pteraster affinis Smith	W. coast of S. Africa. 31° 14′ S. 16° 37′ E.	272	149	Polyzoa and rock	2	AFR 728

Species.	Locality.	Depth in Metres.	Depth in Fathoms.	Nature of Bottom.	No.	Stat. No.
Diplopteraster multipes (Sars)	S. of the Cape. 35° 15′ S. 18° 39′ E.	547	299	. .	1	AFR 831
	W. coast of S. Africa. 32° 37′ S. 16° 31′ E.	530	290	Green sand	1	AFR 700
	W. coast of S. Africa. 31° 30′ S. 17° E.	366	200	. .	1	AFR 725
	W. coast of S. Africa. 31° 44′ S. 16° 13′ E.	457	250	Green mud and sand	1	AFR 716
Cosmasterias felipes (Sladen)	W. coast of S. Africa. 30° 13′ S. 15° 17′ E.	263	144	Grey sand and rock	1	AFR 761
	45 miles N.W. by N. of Cape Town.	329	180	. .	1	TRA 13
	S. of the Cape. 36° 25′ S. 21° 08′ E.	177	97	Sand	1	AFR 945
	N.W. of Cape Town. 32° 34′ S. 17° 03′ E.	318	174	Green mud.	2	AFR 688
Marthasterias glacialis rarispina (Perrier)	False Bay. 34° 07½′ S. 18° 31′ E.	27–28	15	Rock	2	FB 1053
	Off Danger Point.	37	20	Rock	1	AFR 865
Marthasterias glacialis africana (M. & Tr.)	Table Bay. 33° 48′ S. 18° 24′ E.	10–12½	5–6	Stones and shell	1	TB 82

Sclerasterias stenactis (H. L. Clark)	S. of the Cape. 36° 44′ S. 21° 18′ E.	201	110	Grey sand	1	AFR 950
Perissasterias polyacantha H. L. Clark	45 miles N.W. by N. of Cape Town.	357	195	. .	1	TRA 3
	W. coast of S. Africa. 30° 42′ S. 15° 59′ E.	201	110	Light green sand	1	AFR 736
Brisinga cricophora Sladen	W. coast of S. Africa. 31° 23′ S. 16° 30′ E.	366	200	Dark mud and rock	3 pieces	AFR 729
Ophiuroidea.						
Astrothorax papillata (H. L. Clark)	34° 39′ S. 18° 42′ E.	168	92	Green mud	1	AFR 882
Astrocladus euryale Retzius	Between the Heads, Knysna Lagoon.	11½	6	Rock	1	KNY 58
Asteronyx loveni M. & Tr.	W. coast of S. Africa. 31° 44′ S. 16° 13′ E.	457	250	Green sand and mud	2	AFR 716
Ophioscolex dentatus Lyman	W. coast of S. Africa. 31° 14′ S. 16° 37′ E.	272	149	Polyzoa and rock	5	AFR 728
Ophiomyxa vivipara var. *capensis* Mortensen	W. coast of S. Africa. 32° 38′ S. 16° 52′ E.	347	190	Clay and sand	1	AFR 691
Ophiomitrella corynephora (H. L. Clark)	W. coast of S. Africa. 30° 02′ S. 15° 02′ E.	364	199	Green sand	5	AFR 743
Ophiactis carnea (Ljungman)	Off Fishoek, False Bay.	9	5	Sand	2	FB 1072
	Off Fishoek, False Bay.	8	4½	Sand	2	FB 1073
	False Bay. 34° 07½′ S. 18° 31′ E.	27–28	15	Rock	3	FB 1053
	Off Blaauberg, Table Bay.	9	5	Sand and rock	1	TB 90

Species.	Locality.	Depth in Metres.	Depth in Fathoms.	Nature of Bottom.	No.	Stat. No.
Ophiactis plana Lyman	South of the Cape. 35° 09′ S. 19° 02′ E.	207	113	..	5	AFR 835
Amphiura incana Lyman	Fishoek Bay, False Bay.	8	4½	Sand	6	FB 1058
Amphiura capensis Ljungman	False Bay. 34° 07½′ S. 18° 31½′ E.	23–24	13	Shingle	1	FB 1054
Amphiura atlantica var. *dilatata* Lyman	Data not available.	..	..	..	1	AFR 798
Amphiura acutisquama sp. n.	Data not available.	..	..	..	1	AFR 798
Amphiura Simonsi sp. n.	False Bay. 34° 08′ S. 18° 29¼′ E.	27–28	15	Fine shingle	1	FB 1056
Amphipholis squamata (D. Ch.)	Main Channel, Knysna Lagoon.	2–6	1–3	Smooth, loose Zonaria	1	KNY 7
	Table Bay. 33° 52′ S. 18° 28′ E.	15½	8	..	1	TB 87
	Off Fishoek, False Bay.	8	4½	Sand	1	FB 1073
Ophiopsila seminuda sp. n.	False Bay. 34° 08′ S. 18° 29¼′ E.	27–28	15	Fine shingle	1	FB 1056
Ophiothrix aristulata Lyman	South of the Cape. 36° 44′ S. 21° 18′ E.	201	110	Grey sand	2	AFR 950
	W. coast of S. Africa. 30° 13′ S. 15° 17′ E.	263	144	Grey sand and rock	4	AFR 761

Ophiothrix triglochis M. & Tr.	½ mile N.E. of Robben Id., Table Bay.	11	6	Sand	8	TB 83
	Fishoek Bay, False Bay.	7–9	4–5	Sand	5	FB 1058
	False Bay. 34° 07½′ S. 18° 31′ E.	27–28	15	Rock	2	FB 1053
	Main Channel, Knysna Lagoon.	2–6	1–3	Loose Zonaria	1	KNY 7
Ophiura costata Lyman	W. coast of S. Africa. 31° 14′ S. 16° 37′ E.	272	149	Polyzoa and rock	3	AFR 728
Echinoidea.						
Stereocidaris excavata Mortensen	S. of the Cape. 36° 25′ S. 21° 08′ E.	177	97	Sand	1	AFR 945
Salmacis bicolor (L. Agassiz)	The shipping channel, Durban Bay.	..	..	..	1	NA 171
Parechinus angulosus H. L. Clark	Table Bay. 33° 49′ S. 18° 27½′ E.	15	8	Sand and rock	2	TB 81
	Table Bay. ½ mile N.E. of Robben Id.	11	6	Sand	2	TB 83
	False Bay, 1 mile off Fishoek Bay.	22	12	Sand	juv. 2	FB 1059
	Knysna Lagoon.	2–6	1–3	Muddy sand	juv. 12	KNY 6
Echinus Gilchristi Bell	W. coast of S. Africa. 32° 34′ S. 17° 29′ E.	227–230	124–126	Dark green mud and sand	1	AFR 685–6

Species.	Locality.	Depth in Metres.	Depth in Fathoms.	Nature of Bottom.	No.	Stat. No.
Echinodiscus bisperforatus (Leske)	Leisure Isle, Knysna Lagoon.	L.W.S.	L.W.S.	Muddy sand	2	KNY 26
Brissopsis lyrifera (Forbes)	S. of the Cape. 35° 18′ S. 18° 50′ E.	267	146	. .	1	AFR 833
	W. coast of S. Africa. 31° 30′ S. 16° 03′ E.	459	251	Yellow sand, clay, rock	2	AFR 730
Spatangus capensis Döderlein	W. coast of S. Africa. 30° 42′ S. 15° 59′ E.	201	110	Light green sand	1	AFR 736
Echinocardium cordatum (Pennant)	Leisure Isle, Knysna Lagoon.	L.W.S.	L.W.S.	Muddy sand	juv. 4	KNY 26
	False Bay, 1 mile off Fishoek Bay.	22	12	Sand	1	FB 1059
Spatagobrissus mirabilis H. L. Clark	False Bay. 34° 09½′ S. 18° 24′ E.	26½	15	Fine sand	juv. 1	FB 1067
Crinoidea.						
Comanthus wahlbergi (J. Müller)	False Bay. 34° 09′ S. 18° 27′ E.	22	12	Sand	7	FB 1069
	False Bay. 34° 10′ S. 18° 28′ E.	23½	13	Sand and Lithothamnion	2	FB 1064
	False Bay. Off Fishoek Bay	15	8	Shell	4	FB 1060

Tropiometra carinata (Lamarck)	False Bay. 34° 09′ S. 18° 27′ E.	22	12	Sand	1	FB 1069
	False Bay. 34° 09′ S. 18° 29½′ E.	9	5	Shell	1	FB 1052
Cyclometra multicirra sp. n. A. H. Clark	W. coast of S. Africa. 30° 15′ S. 14° 57′ E.	461	252	Green sand	1	AFR 759
Annametra occidentalis (A. H. Clark)	Table Bay, off Blaauberg.	9	5	Sand and rock	3	TB 91
	Table Bay. 33° 49′ S. 18° 27½′ E.	15	8	Sand and rock	12	TB 81
	Table Bay. Details not available.	..	..	..	4	TB 96
	False Bay. 34° 09′ S. 18° 27′ E.	22	12	Sand	6	FB 1069
	False Bay. Fishoek Bay.	8	4½	Sand	1	FB 1058

Family **Astropectinidae.**

Dipsacaster Sladeni subsp. *capensis* subsp. n.

(Plate XVII.)

Dipsacaster Sladeni H. L. Clark, 1923, p. 246
„ „ Mortensen, 1933, p. 237.

TRA 12. 45 miles N.W. by N. of Cape Town. 329–357 metres. 2 specimens.

Remarks.—All the specimens of *Dipsacaster Sladeni* from the Cape region that I have seen differ consistently from Alcock's type (which was taken at the Andaman Islands) in having more marginal plates relative to the arm radius. This fact was also observed by H. L. Clark.

For comparison of the proportions I give the following table:

Specimen . . .	TRA 12*a*.	TRA 12*b*.	1904.			Type of *Sladeni*.
			a.	*b*.	*c*.	
Arm radius (in mm.) .	100	93	92	84	120	110
No. of supero-marginal plates . . .	40	37	37	35	42	32*

(The three 1904 columns refer to the specimens sent to Bell and registered in 1904 as *Leptoptychaster Kerguelensis* Smith.)

In my opinion the discrepancy is sufficiently considerable and constant to warrant a subspecific distinction of the South African form.

Family **Goniasteridae.**

Ceramaster patagonicus var. *euryplax* H. L. Clark.

Ceramaster patagonicus var. *euryplax* H. L. Clark, 1923, p. 362, pl. xiv, 1, 2.
Ceramaster patagonicus var. *euryplax* Mortensen, 1933, p. 243.

AFR 723-5-7. 31° 30′ S., 17° E. (W. coast). 366 metres. 1 specimen.
TRA 7. 48 miles W. by S. of Cape Town. 462 metres. 1 specimen.
TRA 13. 45 miles N.W. by N. of Cape Town. 329 metres. 2 specimens.

* Actually the drawing of the type of *D. Sladeni* Alcock (1893, pl. v, 3) shows 33 or 34 supero-marginal plates on the one complete arm included in the figure, although only 32 are mentioned in the text.

Remarks.—I quite agree with Dr. Mortensen that the characters used to separate this variety from *Ceramaster chondriscus* H. L. Clark are variable and the two forms are probably synonymous in spite of superficial differences. The feature of the sub-ambulacral spine being enlarged in the distal part of the arm is clear in one specimen but less obvious in the other three. The shape of the marginal plates also varies considerably with size, as also does the depth of the interbrachial arc, which is shallower in young specimens.

In comparison with the type of *C. patagonicus* (Sladen), from the Magellan Straits, I can find no significant differences in the granulation of the dorsal and marginal plates, the form of the pedicellariae and the adambulacral armature. In fact, the chief distinctions lie in the size and number of the marginal plates and the depth of the interbrachial arc. The largest of the South African specimens has $R = 67$ mm., $R/r = 1{\cdot}86$, and 21 supero-marginals on each side of an arm, whereas the holotype of the South American form has $R = 68$ mm., $R/r = 1{\cdot}58$, and only 15 supero-marginals.

Genus *Toraster* nov. gen.

Diagnosis.—Goniasteridae with centrally bare, more or less convex, dorsal and marginal plates, otherwise covered with rounded granules which conceal the outlines of the plates themselves; secondary dorsal plates appear among the primary ones in older specimens of arm-radius more than 20 mm.; ventro-lateral plates concealed by covering granules; adambulacral plates relatively short with three furrow spines; pedicellariae broad-bladed, the valves narrowing slightly at the base so that the corresponding depressions in the plates bearing them are dumb-bell shaped.

Type and only species: *Astrogonium tuberculatum* Gray.

Toraster tuberculatus (Gray).

Astrogonium tuberculatum Gray, 1847, p. 79.
,, ,, Gray, 1866, p. 10, pl. i, 2.
Pentagonaster tuberculatus Perrier, 1875, p. 222.
Tosia tuberculata Verrill, 1899, p. 161.
,, ,, Fisher, 1911, p. 166.
,, ,, H. L. Clark, 1923, p. 266, pl. ix, 1, 2.
,, ,, Mortensen, 1933, p. 243, pl. x, 5–7.

AFR 723–5–7. 31° 30′ S., 17° E. (W. coast of S. Africa). 366 metres. 1 specimen.

TRA 13. 45 miles N.W. by N. of Cape Town. 329 metres. 2 specimens.

Remarks.—Gray ascribed this species to *Astrogonium* Müller and Troschel, which, as Verrill pointed out (1899), is really a compound of the

four genera *Goniaster*, *Pentagonaster*, *Tosia* and *Hippasteria* of Gray. Verrill placed it in his emended *Tosia*, probably without seeing a specimen of it, for, as Fisher and H. L. Clark both point out, it is clearly not congeneric with the Australian species of *Tosia*, but comes nearer *Plinthaster* Verrill in having secondary dorsal plates in the adult and a similar type of pedicellaria. I fully agree with them that it should be placed in a separate genus which I name *Toraster*.

This genus differs from *Plinthaster* in having numerous granules concealing the borders of the dorsal plates, whereas the latter has much smaller granules in a single series outlining each plate. Another conspicuous point of difference is the presence of much shorter adambulacral plates in *Toraster*, with only three furrow spines compared with the five or six of *Plinthaster*.

Description of the Type.—B.M. Reg. No. 43.6.19.8. Port Natal.

R = 50 mm., r = 26 mm., R/r = 1·9. 14 supero-marginals.

The disk is wide and the short arms taper to an acute angle.

The dorsal plates are convex, and the larger ones along the middle of the rays have a distinct rounded tubercle surmounting them. Surrounding the convex parts of the plates are numerous closely placed granules, hiding the edges of the plates but leaving spaces for the papulae at intervals. On the distal part of the arms, however, the granules are reduced to a single series around the edge of each plate, although interradially, towards the edge of the disk, the plates become so reduced in size and convexity that their bare central area is gradually encroached upon and finally is completely covered by the granules. The plates are very regularly arranged, in almost parallel rows along the arms, except towards the centre of the disk where some interposed secondary plates upset the regularity. This can be seen in Gray's figure (1866, pl. i, fig. 2).

The supero-marginal plates are all rather convex, especially distally. The infero-marginals are almost flat interradially, but similarly become convex towards the ends of the arms. All the marginals are covered with granules except for their central part. The terminal plate is quite large and tapers to a point. The ventro-lateral area is densely covered with rather angular granules hiding the shape and arrangement of the underlying plates. The adambulacral plates each carry three furrow spines 2–3 mm. in length. Behind these come two much thicker and slightly shorter spines, then, after a short space, two smaller spines barely larger than the granules of the ventro-lateral plates which back on to them.* There are only a few pedicellariae present on the dorsal and supero-marginal plates. These lie

* I am at a loss to understand Perrier's quite erroneous statement that there are but two furrow spines, behind which are two single spines on each plate, forming three rows in all. There is no such condition in the type which he was also redescribing.

near the base of the convex part of the plate in a marked depression. The valves are as broad as long, but narrow towards the base.

Variations.—The most conspicuous variation lies in the great enlargement of the distal-most marginal plates in certain specimens, as in some forms of *Pentagonaster* and some other genera of the Goniasteridae. This has been figured by Dr. Mortensen (1933, pl. x, fig. 6), who also shows a photograph of a very large specimen where the regular arrangement of the dorsal plates has been almost completely lost and the secondary plates are much more widespread than in the relatively immature type specimen.

Another variant is the number of the pedicellariae, which is frequently very great, so that there may be two or even more on one plate. The dorsal plates are not always convex but may have quite flat bare areas, raised slightly above the level of the surrounding granules.

Hippasteria phrygiana var. *capensis* Mortensen.

Hippasteria phrygiana var. *capensis* Mortensen, 1933, p. 245, pl. xi, 1.

TRA 12. 45 miles N.W. by N. of Cape Town. 329 metres. 2 specimens.

Remarks.—Although the South African form of *H. phrygiana* habitually possesses relatively small pedicellariae as noted by Mortensen, this variety is not limited to the Southern Hemisphere, for there are at least four other specimens in the British Museum collection from the region of Norway, with R equal to 60–90 mm. which have ventral pedicellariae only about 1·5 mm. in breadth as in these two Cape specimens (R = 85 and 65 mm.). However, most Northern individuals of a comparable size have the pedicellariae at least 3 mm. in breadth and the small form seems to be comparatively rare, whereas in the Southern Hemisphere it appears to be the rule.

Family **Asteropidae.**

Tylaster meridionalis Mortensen.

Tylaster meridionalis Mortensen, 1933, p. 249, pl. xii, 11–13.

AFR 762. 30° 07′ S., 15° 50′ E. (W. coast of Cape Province). 205 metres. Sand and mud. 1 small specimen.

Remarks.—This station is very near the type locality for Mortensen's species (30° 44′ S., 15° 43′ E., 180 fathoms) and agrees with his description, except with regard to the madreporite which is not conspicuously white and also lies nearer to the centre of the disk than to the edge. This, however, is a relatively minor point. The marginal spines form a short fringe to the edge of the disk when seen from above or below, as in the photographs of the type.

It is a surprising and a rather suspicious fact that from the same station should come a large specimen which is clearly the nearly related *Spoladaster* (*Cryaster*) *brachyactis* H. L. Clark. This suggests that, in spite of the generic difference instituted by Dr. Mortensen, a series of intermediate-sized specimens may show the two species to be synonymous and that the apparent differences are due to the varying degree of development of the spines and plates of the skin, which is probably correlated with the age. The type of *Tylaster meridionalis* has R = 28 mm.

Spoladaster brachyactis (H. L. Clark).

Culcita veneris Bell, 1905, p. 248.
non ,, ,, Perrier, 1879, p. 48.
Cryaster brachyactis H. L. Clark, 1923, p. 293, pl. xi, 1–2.
,, ,, Mortensen, 1933, p. 249, pl. xii, 14.
Spoladaster brachyactis Fisher, 1940, p. 136.

AFR 762. 30° 07′ S., 15° 50′ E. (W. coast of Cape Province). 205 metres. 1 specimen.

Remarks.—The disk is very inflated but measures about 90–100 mm. in diameter and R = approximately 80 mm., compared to 40 mm. in the type. The chief difference from H. L. Clark's description lies in the fact that there are numerous ventro-lateral spines, arranged irregularly and each enclosed in a sheath of skin, whereas the type apparently has these areas quite naked. There are several similar spines in some of the ventral interradii of Bell's South African specimen from False Bay which has R = 58 mm., although Mortensen describes them as being quite smooth.

Culcita veneris Perrier (1879), from St. Paul Island, which I think is probably a *Spoladaster*, has numerous ventro-lateral spines, but those adjacent to the adambulacral grooves are arranged in distinct rows; the diameter of the type is given as 12–13 cm. so that the arm radius would be about 90–100 mm. Whether smaller specimens from St. Paul also have such well-developed ventro-lateral spines is a matter of some interest. Judging from the three known specimens from South Africa, such spines only appear with advancing age but their development may be a case of individual variation.

Family **Echinasteridae.**

Poraniopsis capensis H. L. Clark.

Poraniopsis capensis H. L. Clark, 1923, p. 289, pl. xv, 3, 4.

AFR 755. 29° 16′ S., 14° 48′ E. (W. coast of Cape Province). 238 metres. 1 specimen.

$R = 50$ mm., $r = 25$ mm., $R/r = 2$.

Remarks.—This specimen is almost twice as large as the type, and the spines are proportionally bigger so that the larger ones are about 4 mm. in length. The supero-marginal spines are well developed and arranged in a distinct row along the edge of the body. They taper to a sharp point. The infero-marginal series is also conspicuous and interbrachially arches inwards, so that the intermarginal papular areas are large, like those on the dorsal side. The infero-marginal spines are very flattened, and distally there may be two on one plate. Each adambulacral plate has two spines, also flattened, of which the inner one is the smaller. Dorsally an irregular carinal series of spines can be detected, but otherwise there seems to be no regularity in the arrangement.

The discrepancies between these remarks and the description of the type can all be attributed to the greater size of this specimen.

Henricia studeri (Perrier).

Cribrella studeri Perrier, 1891, p. 102, pl. ix, 2–2*d*.
Henricia studeri Fisher, 1940, p. 163.

AFR 791. No details available. 1 specimen.

$R=43$ mm., $r=10$ mm., $br=11$ mm., $R/r=4{\cdot}3$.

Remarks.—I cannot reconcile this specimen with any species of the Echinasteridae previously known from South Africa but it is almost identical with specimens of *H. studeri* taken by the "Discovery' Investigations in the Falkland Islands and identified as such by Dr. Fisher. It certainly belongs to the *abyssalis-compacta-studeri* group (Fisher, 1940, p. 163), characterized by having "numerous spinelets compactly placed on the plates, especially the marginal, actinal and adambulacral. The actinal series of plates extends well beyond the middle of the ray, sometimes nearly to the tip." The proportions and mesh-size of the dorsal network of plates are much more coarse than in the slender-armed *H. abyssalis*, ten specimens of which have been used for comparison. Only the arrangement of the plates is similar. The average dimensions of the specimens of *H. abyssalis* to hand are: $R=45$ mm., $r=8$ mm., $br=9$ mm., $R/r=5{\cdot}7$.

The presence of papulae on the ventral side prohibits the identification of this specimen as *Echinaster ornatus*, which also differs in having very few, stout adambulacral spines.

It is distinguishable from the other known South African species, *Echinaster reticulatus*, in having multispinous ventro-lateral plates and the dorsal spines slender with thorny ends, whereas in *E. reticulatus* the dorsal spines are described as resembling broken-off tubercles leaving a flat top, so they must be very much more coarse than the spines of this specimen.

The other species in the same group as *H. studeri* and *H. abyssalis* are *H. praestans* (Sladen), from the Crozet Islands, and *H. compacta* (Sladen), from New Zealand.

I am doubtful whether there is any essential difference between the only specimen of *H. praestans* and *H. studeri*. The type of *H. praestans* was distinguished by Sladen as having a primary and a secondary dorsal reticulation, of larger and smaller plates. Quite possibly this appearance is accounted for by the large size of the specimen. The spinelets are relatively very much smaller than in the South African specimen which I have called *H. studeri*, but this again is probably subject to variation. The other noticeable point of difference is the more attenuated arms of *H. praestans* ($R > 6r$, $R = 88$–90 mm.), those of *H. studeri* having rather blunt ends.

In the light of Dr. Fisher's statement (1940, p. 166) that forms very similar to *H. studeri* have been found in South Australian waters, the presence of such a specimen off South Africa is not so surprising. However, I do not know what to call it other than *Henricia studeri*, so, for the moment at least, I leave it under that name.

Family **Pterasteridae.**

Pteraster capensis Gray.

Pteraster capensis Gray, 1847, p. 83.
" " Perrier, 1875, p. 382.
Retaster gibber Sladen, 1889, p. 481, pl. lxxiv, 5, 6; pl. lxxvii, 7, 8.
" " Ludwig, 1905, p. 65, pl. vi, 6–7.
" *capensis* Bell, 1905, p. 250.
Pteraster capensis H. L. Clark, 1923, p. 298, pl. ix, 3–4.
" " Mortensen, 1933, p. 267, text-fig. 9, pl. xiv, 1–3.
" *gibber* Fisher, 1940, p. 197.

AFR 765. 29° 31′ S., 15° 17′ E. (W. coast of Cape Province). 186 metres. 1 specimen.

AFR 791. Position not available. 1 specimen.

AFR 728. 31° 14′ S., 16° 37′ E. (W. coast of Cape Province). 272 metres. 1 specimen.

AFR 691. 32° 38′ S., 16° 52′ E. (W. coast of Cape Province). 347 metres. 1 specimen.

Remarks.—I cannot agree with Perrier in his statement that the type specimen has a wide-meshed reticulum over the dorsal surface. The specimen is dry, and the parts of the supra-dorsal membrane not supported by paxillar spinelets are sunken and appear darker than those parts which are elevated by the spinelets. The result of this is to produce an irregular effect of dark patches, surrounded by lighter bands, but there is no real

reticulum comparable to that of *Euretaster cribrosus* (von Martens). In spirit specimens of similar size (*i.e.* R = 45 mm.), the supra-dorsal membrane has likewise thickened to such an extent as to completely mask any reticulation. However, in the young sea-star up to a size of about R = 30 mm. there is a more or less clearly visible network which may be very conspicuous, as in Sladen's drawing of *Retaster gibber* (1899, pl. lxxiv, 5), or barely discernable.

H. L. Clark states that *P. capensis* has only a single central paxillar spinelet in contradistinction to *P. tesselatus* Ives, from the N.W. American coast. However, in several of the dozen specimens I have seen there are two or more central spinelets on many of the paxillae, though in most examples the number is predominantly one. This disposes of the only notable difference between *P. gibber* from South America and *P. capensis*, which I consider to be synonymous. Possibly *P. tessalatus* should also be included, judging from H. L. Clark's observations; however, I have not seen any material of that species.

Pteraster affinis E. A. Smith.

Pteraster affinis Smith, 1876, p. 108.
„ „ Smith, 1879, p. 275.
„ „ Mortensen, 1933, p. 397.

AFR 728. 31° 14′ S., 16° 37′ E. (W. coast of Cape Province). 272 metres. 2 specimens.

One of these specimens has a tricarinate superoral spine, while in the other it is merely cylindrical. The types (from Kerguelen), as observed by Mortensen, are also variable in this respect.

Family **Asteriidae.**

Marthasterias glacialis var. *rarispina* (Perrier).

Asterias rarispina Perrier, 1875, p. 62.
Marthasterias rarispina H. L. Clark, 1923, p. 305.
„ *glacialis rarispina* Mortensen, 1933, p. 273, pl. xvi, 2–3.

FB 1053. 34° 07′ S., 18° 31′ E. (False Bay). 49–51 metres. 2 specimens.

AFR 865. Off Danger Point. 37 metres. 1 specimen.

Remarks.—I fully agree with Dr. Mortensen that the South African form of *Marthasterias*, with the dorso-lateral spines reduced or absent, is no more than a variety of *M. glacialis*. One of the False Bay specimens has some dorso-lateral spines present, but these are completely lacking in the other two. All three, however, have the carinal row of spines regularly

zigzagging distally, a peculiarity I have not seen in those few North Atlantic specimens which similarly have no dorso-lateral ones.

The ten "Challenger" specimens from Simon's Bay, named *Asterias africana* by Sladen, are all *rarispina* and eight of them have no dorso-lateral spines. The trend for reduction of the dorsal spines seems to be correlated with the latitude, for most specimens in the British Museum from Madeira and the Azores have no dorso-lateral spines, whereas a smaller proportion of specimens from farther north share this condition.

OPHIUROIDEA.

Family **Asteronychidae.**

Asteronyx loveni Müller and Troschel.

Asteronyx loveni Müller and Troschel, 1842, p. 119.
,, ,, Mortensen, 1933, p. 301.

AFR 716. 31° 44′ S., 16° 13′ E. (W. coast of Cape Province). 457 metres. 2 specimens.

These two specimens are both parasitized by Copepods, which project from the genital slits.

Family **Ophiacanthidae.**

Ophiomitrella corynephora H. L. Clark.

Ophiomitrella corynephora H. L. Clark, 1923, p. 322, pl. xix, 5, 6.
,, ,, Mortensen, 1933, p. 331, text-figs. 48, 49.

AFR 743. 30° 02′ S., 15° 02′ E. (S.W. of the Orange River mouth). 364 metres. 5 specimens.

Remarks.—This locality extends the known range somewhat farther north. Probably more collecting off the coast of South-West Africa will show the true northern extent of the ranges of this and many other species known at present only from the west coast of Cape Province.

There is some variation in the proportions of arm-length and disk diameter, the measurements being as follows:

Specimen	1.	2.	3.	4.	5.	Type.
Disk diameter, in mm. .	10	7·5	6	8	8	8
Arm-length, in mm. . .	26	16	18	31	26	30
Ratio	2·6	2·1	3·0	3·9	3·3	3·8

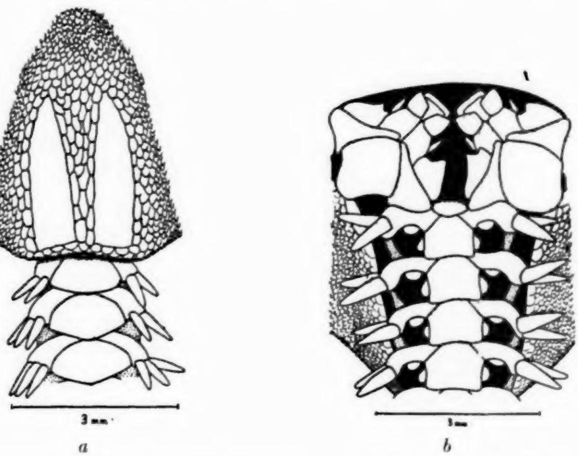
Family **Amphiuridae.**

Amphiura acutisquama sp. n.

(Text-fig. 1, *a*, *b*.)

AFR 798. W. coast of South Africa between 183 and 550 metres. (Details not available.) 1 specimen.

Unfortunately the disk has been squashed flat and the arms are all broken. The disk diameter is now 15 mm., while the arm-length probably exceeded 100 mm., judging by the degree of taper of the broken pieces.



TEXT-FIG. 1.—*Amphiura acutisquama* sp. n. Type. The base of an arm and adjacent parts of the disk in (*a*) dorsal view, and (*b*) ventral view (the oral shield on the right is the madreporite).

Diagnosis.—A species of *Amphiura* characterized by having minute angular scales covering the disk, only becoming smooth and a little larger around the radial shields and genital scales; two tentacle scales; one massive, double-pointed distal oral papilla.

Description.—The disk is covered with very fine pointed scales standing up from the surface so as to produce a rough texture, except around the radial shields where the scaling is somewhat coarser and smoother. In the centre of the disk one plate is just discernible as being slightly larger than the surrounding scales, but its diameter is only 0·2 mm. No enlarged primary radial plates are visible. The radial shields measure 3 mm. in length and just under 1 mm. in width. The distal edge is straight, while

the proximal half tapers to an angle. The two shields of each pair are quite separated by a band of scales of which there are at least three rows at the narrowest (distalmost) part. The ventral side of the disk is completely covered with very fine scales similar to those of the dorsal surface. Interradially these are rather angular but towards the genital slits they are flatter and increase in size a little.

The oral shields are slightly longer than wide, with a blunt proximal angle and a narrowed distal lobe. The madreporite is very swollen and almost circular in outline. The adoral shields are narrow inwardly and do not meet interradially. Outwardly they have a narrow process separating the oral shield from the first side arm-plate. The infra-dental papilla is quadrangular when seen from below, while the distal papilla is relatively massive and usually has a double apex.

The dorsal arm-plates are hexagonal, with a very obtuse distal angle and divergent side edges. The first two or three are separate, but the rest tend to overlap to some extent. The ventral arm-plates are pentagonal with a slightly truncated proximal angle, which is also a little swollen. The distal edge is usually straight but may be slightly convex on the proximal plates.

Near the disk there are five smooth arm-spines, each tapering to a point. However, by about the thirtieth segment the number has been reduced to three.

There are two tentacle scales.

Remarks.—The *Amphiura* species most closely related to this one is, I think, *A. princeps* Koehler (1907), from the Magellanic region. Mortensen's figure in his "Discovery" Report (1936, p. 286) shows that the scaling of the ventral side of the disk is quite comparable with that of *A. acutisquama*, except that the scales apparently do not increase in size towards the genital slits. Other similarities lie in the shape of the arm-plates and oral shields. However, the distal oral papilla is less massive in *A. princeps*, and the first ventral arm-plate is much more reduced in size than in the South African species. Also, the disk scales on the dorsal side are relatively more coarse in *A. princeps* and there is a distinct central rosette of larger plates.

Koehler's photographs (1914, pl. 8, figs. 5, 6) of the type of *A. otteri* Ljungman, from the North and Central Atlantic, have a very great resemblance to the present specimen, especially with regard to the shape of the radial and oral shields, the arm-plates and ventral disk scales. However, here again the dorsal disk scales are larger and more rounded, while proximally there are six or seven arm-spines (of which one is hooked) rather than five spines as in *A. acutisquama*.

There are several other *Amphiura* species with two tentacle scales, one distal oral papilla and the ventral side of the disk completely covered with

scales: these include *A. palmeri* Lyman, *A. Joubini* Koehler, *A. rapida* Koehler, *A. complanata* Ljungman, *A. serpentina* Lütken and Mortensen, and *A. bellis* Lyman, besides others, such as *A. belgicae* which have larger disk scales. The first four of these species are distinguished by having one or more of the arm-spines conspicuously curved or hooked, besides differing in other minor characters. *A. bellis*, which comes from Japan, has smoother disk scales, and the two radial shields of each pair converge distally and almost meet.

Lütken and Mortensen's work on *A. serpentina* from the Gulf of Panama (1899, p. 143, pls. viii, 1–8; ix, 1–2) shows how variable certain characters can be, particularly the size of the disk scaling, the presence or absence of distinctly larger primary plates in a rosette, and the form of the oral papillae and oral shields. The very different appearances of the varieties they have illustrated suggest that some of the many other species of *Amphiura* described will eventually be found to be only synonyms. *A. serpentina* itself can be very similar to *A. acutisquama*, but their geographical separation precludes any likelihood that they are identical species.

This specimen answers fairly well to Ljungman's description of *A. candida* from Mozambique (1867, p. 318) except that the latter has spine-like distal oral papillae, the disk incised above each arm insertion, and a rosette of larger plates in the middle of the disk (a feature which may be variable as in *A. serpentina*). However, it is improbable that they are the same species, for the fauna west of False Bay is rather sharply differentiated from that to the north-east of Durban and few species are common to both. Mortensen has declared *A. candida* a *species delenda*, since the type is unrecognisable. It is unfortunate that Koehler should have re-described the species from a Japanese specimen, which is surely not the same.

This new species is easily distinguished from the other known *Amphiurias* previously described from the Cape region, by the presence of two tentacle scales and the complete covering of the ventral side of the disk with scales. From *A. incana*, which also possesses these characters, it differs most obviously in the very much smaller disk scales.

Amphiura Simonsi sp. n.

(Text-fig. 2, *a–c*.)

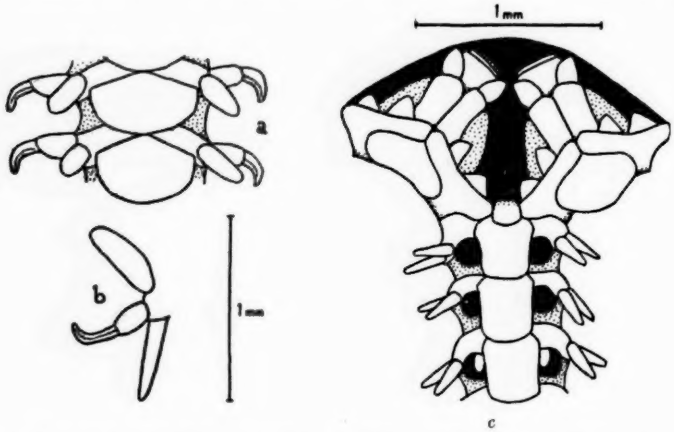
FB 1056. 34° 08′ S., 18° 29′ E. (False Bay). 27–28 metres, shingle bottom. 1 specimen.

Unfortunately the disk of this specimen is missing, so it is possible that the species may belong to a different genus of the Amphiuridae. However,

the remaining characters show that it is distinct from any previously described species.

Diagnosis.—A species of *Amphiura*, with one rounded tentacle scale and two distal oral papillae, placed on the adoral shield, *not* on the oral plate; the middle arm-spine conspicuously hooked in the distal part of the arm, where the spines number but three.

Description.—The oral shields are short, with an obtuse proximal angle and rounded sides. The madreporite is swollen and has a slight distal lobe.



TEXT-FIG. 2.—*Amphiura simonsi* sp. n. Type. (*a*) Dorsal view of two arm segments from about the middle of an arm, (*b*) side view of the arm spines from a segment in the same region, and (*c*) ventral view of the base of an arm and part of the mouth apparatus (the oral shield on the right is the madreporite).

The adoral plates are quite wide internally and meet broadly. They have an extension separating the oral shield from the first lateral arm-plate. The oral plates are narrow, about half as long again as wide and without a depression between them. The two infradental papillae on each jaw angle are conical, with the apices rather divergent. Distally there are two oral papillae on each adoral shield, although the base of the inner one may be partly on the oral plate. These papillae are short and triangular in outline. They are widely separated from the infradental pair by the length of the oral plates.

The first ventral arm-plate is quadrangular in shape, with a rounded distal edge. The following plates similarly have a convex outer side but are a little larger than the first one. They are as long as broad with almost straight sides. Distally, however, the ventral arm-plates are shorter and the outer edge becomes somewhat concave.

Proximally there are five arm-spines, but the two uppermost are lost in turn in the first half of the arm. All these spines are straight at first, but a short distance out from the disk the second spine from below takes on a swollen rugous form with a small distally-directed hook at the end. Further out on the arm this hook increases progressively in size, becoming hyaline at the same time, so that by about the fortieth segment, where the spines have been reduced to three in number, the hook is clearly visible with the naked eye. The upper spines are rather spatulate in form while the lowermost one is long and cylindrical and tapers gradually.

The length of the arm is between 70 and 80 mm., which is relatively long as the jaw apparatus is not very massive.

The first two pairs of tentacle pores have no scales but those beyond have a single oval one.

Remarks.—Dr. Mortensen might perhaps consider this species to be an *Amphiodia* since there are two outer oral papillae, but as these are not placed so as to allow complete closing of the mouth it is difficult to relate it to that genus as defined by Verrill (1899 *a*). Some species of *Amphiodia*, such as *A. affinis* Studer (1885), can have adoral shields, arm-plates and tentacle scales similar to those in this specimen, but the two distal oral papillae are situated on the oral plates in a continuous series with the infradental one.

This species is linked with a few others such as *Amphiura diomediae* Lütken and Mortensen, *A. Eugeniae* Ljungman and *A. ascia* (Mortensen), which also have two distal papillae based on the adoral shields, but it differs from these particularly in having only one tentacle scale, whereas *A. diomediae* and *A. Eugeniae* have two and *A. ascia* has none. The latter is otherwise very similar to the False Bay specimen except for the more numerous arm-spines, one of which is bihamulate, and the spinous second oral papilla. The type is from Angola.

Finally, mention should be made of *Amphiura concinna* Koehler (1904) which is the only other *Amphiura* species having two distal oral papillae (on the adoral shields) and only one tentacle scale, but here again the second oral papilla is spine-like and also the adoral shields do not meet interradially. Anyway this species was taken by the "Siboga" expedition in 2081 metres.

It is to be hoped that further material will soon be available so that the characters of the disk may be made known and the species fully described.

Family **Ophiocomidae.**

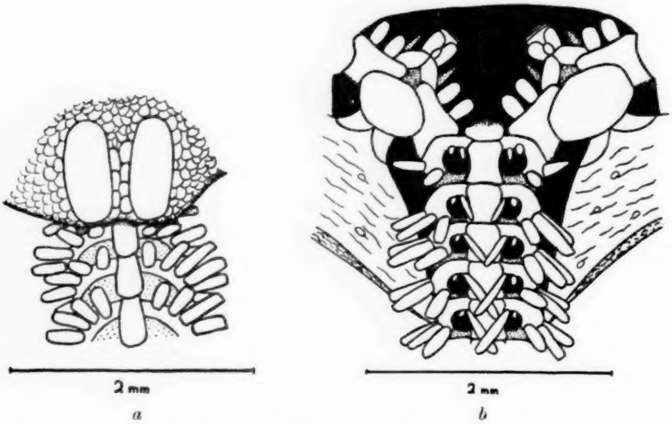
Ophiopsila seminuda sp. n.

(Text-fig. 3, *a–b*.)

FB 1056. 34° 8′ S., 18° 29′ E. (False Bay). 27–28 metres. 1 specimen.

Disk diameter = 4 mm. All the arms are broken towards the ends but were probably about 30 mm. in length.

Diagnosis.—A species of *Ophiopsila* with the ventral side of the disk covered with bare skin having only a few scattered plates; only three



TEXT-FIG. 3.—*Ophiopsila seminuda* sp. n. Type. The base of an arm and adjacent parts of the disk in (*a*) dorsal view, and (*b*) ventral view (the oral shield on the right is the madreporite).

dental papillae of which two are large and resemble the infradental papillae of an *Amphiura*.

Description.—The disk is covered with fine scales increasing in size around the radial shields, which are about a third of the disk radius in length and about two and a half times as long as wide. The shields of each pair lie parellel and are completely separated by two rows of scales. There is a sharp dividing line between the upper and lower sides of the disk, the ventral side being naked except for a few scattered, almost indistinguishable plates. The genital slits, as usual in the genus, are large.

The oral shields are wider than long, with very obtuse proximal and distal angles. The madreporite is almost hexagonal, with short straight sides. The adoral shields do not meet interradially, but are enlarged

outwardly so as to separate the oral shields from the first lateral arm-plates. Two large flattened oral papillae with rounded ends are borne on each adoral plate. Above these a long narrow oral tentacle scale can be seen.

There are four or five large teeth in each series and below these two large tooth papillae with a smaller third one in front. At first sight this arrangement suggests an *Amphiura* but for the third papilla.

The dorsal arm-plates are almost twice as long as wide, being relatively narrow. Each slightly overlaps the next distal one. The lateral plates are narrow and leave a considerable part of the side of each joint covered only by skin. The ventral arm-plates are a little longer than wide, with slightly projecting distal corners and concave sides.

Proximally there are seven spines on each of the quite conspicuous arm-plates. These spines are very stout with little or no tendency to taper and are somewhat rugous at the ends. The lowest is much the largest, both in thickness and in length, being nearly twice the length of a segment, whilst the uppermost is only half as long.

The first inner tentacle scale is thin and fairly short, but the dimensions increase in the following segments so that, from the fourth one onwards, the length of these scales exceeds that of a joint, and the two inner scales of each segment cross over one another. They are considerably flattened and widen out in the middle, tapering towards the ends. The outer tentacle scale is always relatively small.

The colour is completely lost except for a dark blue line made by the dorsal arm-plates on the proximal part of the arm.

Remarks.—This species is almost at the limit of reduction of the dental papillae in the genus *Ophiopsila*, these being replaced by teeth except for three papillae of which two are enlarged. Most of the other species of the genus have only two or three, if any, teeth and numerous tooth papillae below them. There is most affinity in this respect with *O. maculata* Verrill (1899 *b*) and *O. fulva* Lyman (1878), both from the West Indies. However, unlike these species, the tooth papillae do not form a continuous series with the oral papillae in this specimen, but are distinctly separated from them much as the infra-dental papillae of an *Amphiura* are separated from the distal papillae. This arrangement is closer to that found in other *Ophiopsila* species such as *O. aranea* Forbes.

This most interesting species is easily distinguished from others of the genus by the ventrally bare disk and the small number of tooth papillae, together with the form of the adoral plates and the number of arm-spines.

ECHINOIDEA.

Family **Spatangidae.**

Spatagobrissus mirabilis H. L. Clark.

Spatagobrissus mirabilis H. L. Clark, 1923, p. 402, pl. xxiii.

FB 1067. 34° 9′ S., 18° 24′ E. (False Bay). 26 metres. 1 specimen.

This specimen is, unfortunately, a young one with a major horizontal diameter of only 29 mm. However, it is most interesting in being the first known specimen complete with spines, for the holotype is a large dead test.

It was sent, at his request, to Dr. Mortensen, who is much better qualified than I to describe its spines and pedicellariae, for inclusion in the last volume of his great Monograph of the Echinoidea.

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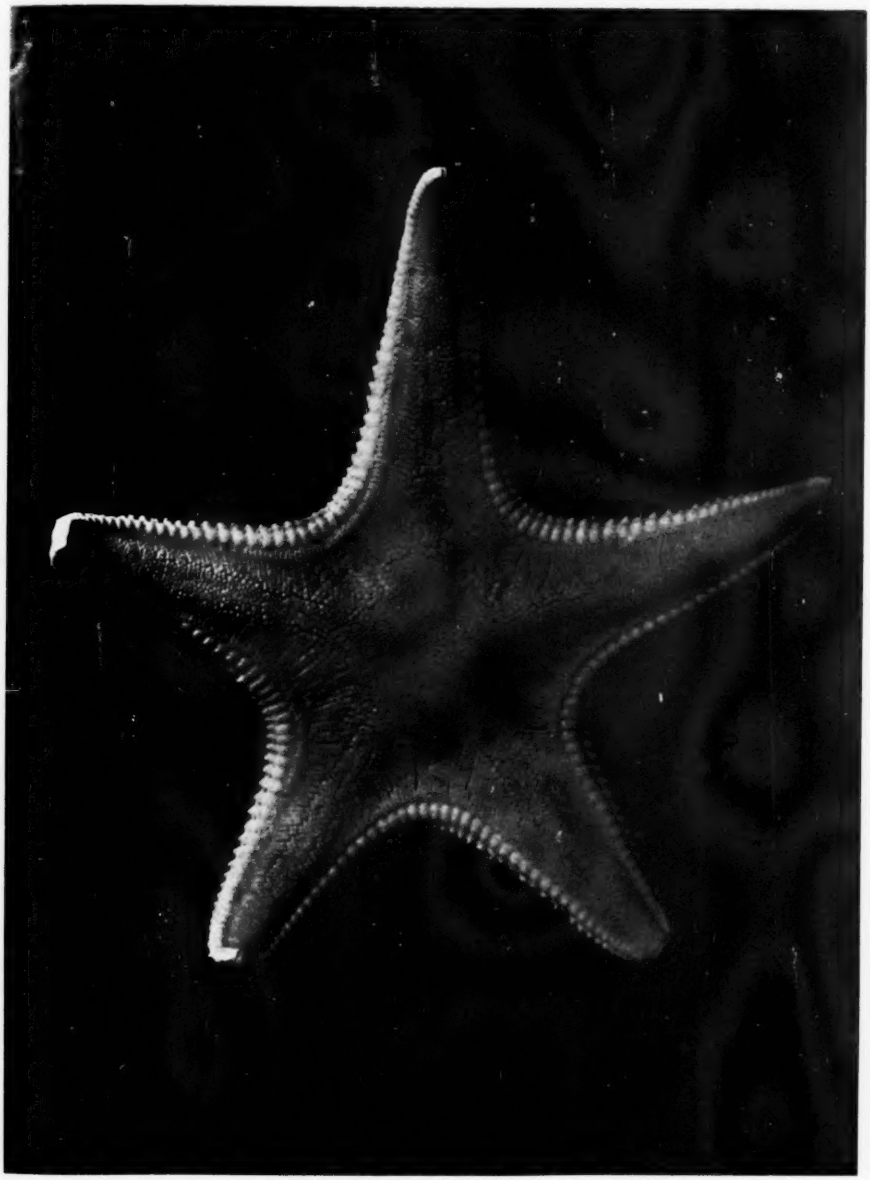

Dipsacaster Sladeni subsp. *capensis*.
subsp. n. B.M. Reg. No. 1904. 4.26.4. Dorsal view. × 1.

Ailsa M. Clark. *Neill & Co. Ltd.*

THE ORIGIN AND DEVELOPMENT OF THE EMBRYO SAC AND YOUNG EMBRYO OF *LORANTHUS RUBROMARGINATUS* ENGLER.

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(Communicated by R. S. Adamson.)

(With Plates XVIII–XXI and three Text-figures.)

(Read September 20, 1950.)

Synopsis.

The floral structure and its development in *Loranthus rubromarginatus* resembles that of the other Loranthoideae in which no placenta is formed.

The haploid chromosome number is nine.

At the base of a small ovarian cavity a number of archesporial cells are formed hypodermally. These differentiate into the megaspore mother-cells. Megasporogenesis is normal.

Loranthus rubromarginatus is suspected to be apomictic. The upper megaspore of the linear tetrad may, however, develop into an embryo sac. The mature embryo sac is up to 35 mm. in length. The apex contains two synergids, an egg, and an upper polar nucleus; only one large nucleus is found in the basal end.

The first division of the egg is longitudinal. A long 2- or 4-rowed suspensor pushes a two-celled embryo down the tubular embryo sac into the endosperm. Only one of three or more embryos reach maturity.

The endosperm is formed from divisions of the large basal nucleus and probably has the diploid chromosome number. The first endosperm cells resemble the antipodals of other angiosperm embryo sacs.

CONTENTS.

I. Introduction.

Like the closely allied Santalaceae, the Loranthaceae reveal a peculiar structure in their flower morphology, especially in the gynoecium. The simplification of the ovules and the placenta, as found in the Santalaceae, is more advanced in the Loranthaceae, many genera possessing no placenta or ovules, the latter being reduced to embryo sacs which arise at the base of a minute ovarian cavity (1, 12, 15, 16, 17, 18, 19). Together with this simplification the structure of the embryo sac is peculiar. This was already noticed by Griffith in 1843 in the so-called *Loranthus bicolor* and *L. globosus*. His investigations were followed by those of Hofmeister, van Tieghem and Treub (18, 19) in the nineteenth century and those of York (20), Billings (1) and Schaeppi and Steindl (16, 17) in the present century. We owe the first clear and correct account on the developmental stages of the Loranthacean reproductive organs to Treub (18, 19).

The origin and development of the embryo sacs are very different in the two sub-families, viz. the Loranthoideae and the Viscoideae. The Loranthoideae have monosporic embryo sacs which grow up the style to a greater or lesser extent, whereas the Viscoideae have bi- or tetra-sporic embryo sacs which are hook-shaped.

Although intermediate forms exist, the Loranthoideae can be divided into two groups, as far as the placenta or Treub's "mamelon" is concerned, viz. those with a distinct placenta and those without one. To this latter group belongs *Loranthus rubromarginatus*, a South African species parasitising *Protea caffra* at sites north and west of Johannesburg where the material was collected.

Methods.

After quickly removing the perianth of the buds and flowers and cutting away one side of the receptacle-ovary tissue, the material was fixed at reduced pressure in (*a*) Flemming's strong chrom-osmo-acetic fixative, (*b*) Carnoy's fixative, or (*c*) Navashin's fixative (modified). The Navashin fixative was found to be the most satisfactory.

The material was microtomed at thicknesses varying from 10 μ to 18 μ according to the stage of the material. Heidenhain's iron hematoxylin or crystal violet, combined with orange G, were the chief stains employed. All drawings were made with the aid of a camera lucida.

II. Notes on the Androecium and Microsporogenesis.

The stamens are of the arrow type, differing from the other Loranthoideae, especially *Lepeostegeres*, *Scurrula*, and *Amyema*, in which there is a gradual

transition between the anther and filament (16). Unlike genera such as *Macrosolen, Elytranthe, Dendrophthoe,* and *Taxillus,* the anthers in the bud are not temporarily united but only closely juxtaposed. The pollen sacs are not secondarily divided into compartments by sterile tissue as was found in many other genera (12, 16).

When buds approach the 10-mm. length, differentiation of the sporogenous tissue in the anthers begins. (Normally the young flower buds begin to appear in May and June, maturing during July and August, and flowering in September and October. Ripe fruits are abundant in November.) Before meiosis starts, the archesporial cells are closely packed and have large nuclei. When meiosis is to begin, however, the cells separate and are loosely arranged so that excellent aceto-carmine squashes were made following the Darlington and La Cour (2) schedule. The anthers of buds having a length of about 10 mm. were used for the squashes.

The meiotic division stages in the anthers of a single bud and even in a single anther were found to differ. Counts were made of buds from several localities. The chromosomes were large and separated well. Both the first and second metaphasic stages were suitable for counting. Nine bivalents are arranged on the metaphase plate during the heterotypic division of the pollen mother-cell (fig. 8 *a*). This haploid number was also found in an Indian species, viz. *Loranthus longiflorus* (7). It appears thus from the observations made on these widely separated species that the basic number of chromosomes in *Loranthus* is nine. Wallformation between the nuclei does not start until after telophase II.

III. Megasporogenesis.

Simplification in the ovary of *Loranthus rubromarginatus,* as in *Scurrula, Taxillus,* and *Dendrophthoe* (16), has gone to the extreme, so that no ovules or placentae are differentiated. Only a small ovarian cavity (ov.c.) is formed which is continuous with a thin stylar canal (fig. 2; Plate XVIII, figs. 4, 5).

The epidermal cells lining the base of the ovarian cavity as well as the cells below them, in the approximately 2 mm. long bud, begin to enlarge and show a larger nucleus and denser cytoplasm than the surrounding cells (Plate XVIII, fig. 4). In buds of a younger stage there is no indication of this differentiation. From the lining of the ovarian cavity no other tissue is differentiated. The hypodermal cells, however, are the archesporial cells (Plate XVIII, fig. 4, ar.c.). Two nucleoli are observable in each nucleus.

Development of the archesporial cells is very slow. Longitudinal sections of an 8 mm. bud reveal that the archesporial cells become loosely arranged and elongated in the direction of the longitudinal axis of the flower.

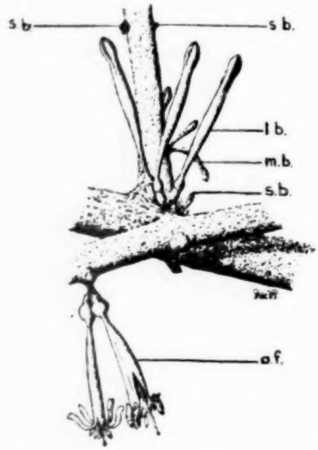

Fig. 1.—*Loranthus rubromarginatus.* Buds and flowers before appearance of the leaves. l.b., large buds; m.b., medium-sized buds; o.f., open flowers; s.b., small buds. (less than × 0·05.)

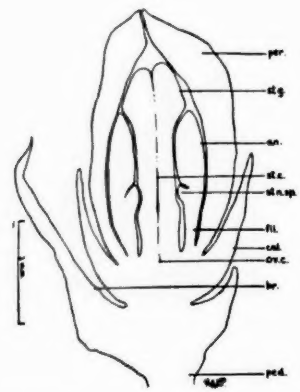

Fig. 2.—*Loranthus rubromarginatus.* A longitudinal section through a ± 3 mm. bud. an., anther; br., bract; cal., calyculus; fil., filament; ov.c., ovarian cavity; ped., pedicel; per., perianth; stg., stigma; st.c., stylar canal; stn.sp., staminal spur. (× 15.)

The longest are about $38\,\mu$ long and less than $10\,\mu$ broad (Plate XVIII, fig. 5). The nuclei lie near the basal end * of the archesporial cells. The nuclei measure about $8\,\mu$ in diameter. Some of these archesporial cells divide transversely to the longitudinal axis of the bud to form two daughter archesporial cells (Plate XVIII, figs. 5, 6).

At a later stage of development these archesporial cells were found to have elongated considerably, some reaching $50\,\mu$ in length. Other archesporial cells had undergone transverse divisions so that rows of four cells could be observed (Plate XVIII, fig. 6). This is distinctly not a linear tetrad of megaspores, the cells being loosely arranged and with their nuclei in the typical mitotic prophase stage. Each nucleus also possesses two large nucleoli. Disintegration of the cells lining the ovarian cavity sets in at this stage. At the same time, a few cell layers below the archesporial cells, the collenchymatous plate is being differentiated (Plate XVIII, fig. 6; col. pl.). The cellular tissue surrounding the archesporial cells, although having a nucellar function, is perhaps not homologous with a nucellus.

After further elongation the archesporial cells function as the megaspore mother-cells. Instead of the usual one or two megaspore mother-cells differentiated per ovule as in most angiosperms as well as in *Lepeostegeres gemmiflorus* and *Macrosolen cochinchinensis* (16), a large number are formed hypodermally at the base of the ovarian cavity. In this respect *Loranthus* resembles *Helixanthera* and *Dendrophthoe* (12, 16). The meiotic division of the megaspore mother-cell nucleus starts when the bud is about 34 mm. and the megaspore mother-cell about $110\,\mu$ long. The nuclei are large—$25\,\mu$ long and $13\,\mu$ wide—and stain excellently (Plate XVIII, fig. 7). In contrast with the nuclei of the archesporial cells, the megaspore mother-cell nuclei in the prophase stage possess only a single nucleolus. The megaspore mother-cell nuclei in most cases lie near the basal end. Nuclear development in the megaspore mother-cells is not simultaneous (Plate XVIII, fig. 7). Chiasmata were observable in the diplotene stage. The two nuclei in the megaspore mother-cell-like cell on the extreme left of fig. 7 are considered to be the result of a mitotic and not a meiotic division.

Two megaspore mother-cells can occur one above the other (Plate XIX, fig. 8). The nuclei of these two cells are shown in the first meiotic metaphase stage. With difficulty, nine bivalents could be distinguished on each metaphase plate. Since nine was found to be the haploid number, it is thus proved that the megaspores possess the reduced number of chromosomes.

After the first meiotic division of the megaspore mother-cell nucleus a

* Since we are not dealing here with ovules having micropyles, the terms micropylar end and chalazal end do not apply. The terms here used will be the basal end—directed towards the pedicel of the flower; and the upper end—directed towards the stigma.

thin wall is formed between the two sister nuclei, resulting in the formation of a dyad (Plate XIX, fig. 9; dy.). The division of two megaspore mother-cells lying in a row (fig. 8) may result in the formation of two groups of dyads in a row simulating a linear tetrad of megaspores (fig. 9). The dyad nuclei are much smaller than those of the megaspore mother-cells, but the cytoplasm is just as dense. Some sterile archesporial cells undergo a series of mitotic divisions to form rows of cells amongst the megaspore mother-cells and dyads, but are distinguished from the latter by means of their size and structure of the nuclei (Plate XIX, fig. 9; r.c.). Some megaspore mother-cells may degenerate and thus make way for the other developing cells (fig. 9; d.c.).

The homotypic division of the dyad nuclei results in the formation of a linear tetrad of megaspores (Plate XIX, fig. 10). Whereas the megaspore mother-cells and dyads are thin-walled, the megaspores have a fairly thick and conspicuous cell-wall. Megasporogenesis in *Loranthus rubromarginatus* as in *Lepeostegeres gemmiflorus*, *Elythranthe parasitica* and *Helixanthera hookeriana* (16) follows the "Normal-type." * In *Macrosolen cochinchinensis* only a triad is formed in which the four nuclei are distributed (16).

As is apparent from figs. 10 and 11 (Plate XIX) it is the upper megaspore that enlarges and will probably develop into the embryo sac, as in *Elythranthe parasitica* and *Helixanthera hookeriana* (16).

IV. The Development of the Embryo Sac.

The functional megaspore or one-nucleate embryo sac is approximately 60 μ long and 32 μ broad. At this stage the bud, whose developmental stages resemble that of the other investigated genera, is about 40 mm. in length. Enlargement of the embryo sac after this stage is very rapid, and the non-functional megaspores, megaspore mother-cells, dyads and neighbouring cells of the ovarian tissue are squashed. Shortly after enlargement of the embryo sac begins, the nucleus divides to establish the two-nucleate embryo sac. The two nuclei become orientated, one at the upper and the other at the basal end of the embryo sac. The embryo sac is now about 70 μ to 100 μ in length (Plate XIX, fig. 11).

The embryo sac elongates rapidly both upwards into the style and downwards, but the downward growth of the basal end is checked by the shield-shaped collenchymatous plate.

The next stage observed was of a three-nucleate embryo sac, at which stage the embryo sac had nearly obtained its mature length of 25 to 35 mm. The club-shaped apex of the embryo sac in the style contains two nuclei

* Now named by P. Maheshwari the Polygonum type in his book, *An Introduction to the Embryology of Angiosperms*. New York. 1950.

(Plate XX, fig. 13), whereas the basal end contains only a single large nucleus (Plate XX, fig. 12). The embryo sac being extremely long and twining, it was impossible to obtain sections having the whole embryo sac in one section. The embryo sacs also being numerous it could not be ascertained which basal end belonged to a particular apex, but as the various embryo sacs have a similar structure in the basal ends, and also in the apices, there was no difficulty in establishing the exact structure of the embryo sac at the various stages of development. In no embryo sac were there observed more than one nucleus in the basal end at any stage of development. The basal nucleus of the two-nucleate embryo sac undergoes no further development until after embryo formation begins.

The genera investigated by Schaeppi and Steindl, however, included a four-nucleate embryo-sac stage; although in *Macrosolen cochinchinensis* and *Lepeostegeres gemmiflorus* one of the two basal nuclei degenerates, the embryo sac then becoming three-nucleate. The other basal nucleus functions as the lower polar nucleus and fuses with the upper.

The five-nucleate stage, which was expected to follow the three-nucleate stage, was not observed, the next stage found being the mature embryo sac. The upper nuclei of the three-nucleate embryo sac are expected to divide to form the five-nucleate sac, the upper four nuclei of which then differentiate into the egg apparatus and the upper polar nucleus.

The apices of up to nine mature embryo sacs were found in the style of *L. rubromarginatus*. In *Dendrophthoe pentandra*, K. V. Rauch counted twelve egg apparatus (16). The mature embryo sac of *L. rubromarginatus* is from 20 mm. to 35 mm. in length. The basal end is about 130 μ in diameter (Plate XX, fig. 12). The width of the tube up the style is usually 65 μ, but widens again at the apex, which contains the egg apparatus. This apex in the mature embryo sac may be as broad as 175 μ (Plate XX, figs. 14, 15). The egg apparatus is of the normal type consisting of two synergids, a large egg-cell and an upper polar nucleus (Plate XX, fig. 14).

The synergids (fig. 14; syn.) lie at the apex of the embryo sac and partially enclose the upper portion of the large spherical egg. Each synergid is an irregular oblong cell and has a small nucleus which is about 12 μ in diameter. Usually the synergids degenerate early (fig. 14, *a*), but sometimes one synergid may enlarge and resemble the egg-cell, except for its smaller nucleus (fig. 14, *b*); the other synergid degenerates as usual. The egg-cell, which lies below the synergids, is an enormous cell measuring from 50 μ to 70 μ in diameter and contains a nucleus having a diameter of about 35 μ. A number of large vacuoles are found in the cytoplasm of the egg. The upper polar nucleus—there having been no fusion to form a secondary nucleus as in the other genera (16)—lies close to the egg, to which it is

attached by a strand of cytoplasm. The polar nucleus is slightly elongated and may be up to 40 μ long and 30 μ wide (fig. 14; pol.n.).

The only other nucleus in the mature embryo sac is the large nucleus in the basal end of the embryo sac. This nucleus is the largest of all the embryo-sac nuclei, measuring more than 40 μ in diameter (Plate XX, fig. 12). All the embryo-sac nuclei contain only one nucleolus. No antipodals are formed as in *Scurrula atropurpurea* (16).

The embryo-sac development is thus a modification of the "Normal-type," using the terminology of Maheshwari (10, 11).

There is no fusion of the upper polar nucleus with a lower nucleus in *L. rubromarginatus*, as has been described for some other genera (16). In these genera, however, the embryo sacs are much shorter than in *L. rubromarginatus*. In *Macrosolen* and *Lepeostegeres*, for example, the mature embryo-sac apices are found near the junction of the style and ovary, those of *Dendrophthoe* and *Amyema* half-way up the style, and that of *Taxillus* a little above the middle. Even in the two investigated species of *Helixanthera* (12, 16), where the embryo-sac apices are found in the tissue of the stigma, the length of the embryo sac does not exceed 8 mm., whereas that of *L. rubromarginatus* is up 35 mm. The embryo-sac apex of *L. rubromarginatus* is found about three-quarter-way up the style of newly opened flowers. Thus, although it is possible for the upper polar nucleus to fuse with a lower in the other genera, it is highly improbable, if not impossible, that such a fusion can occur in *L. rubromarginatus*.

V. Syngamy.

Except for one case where some pollen from the anthers of the same flower stuck to the style and the base of the stigma, no other instances were found of pollen occurring on the stigma sections. Also no pollen tubes could be distinguished in the stylar tissue. In those Loranthoideae studied by Schaeppi and Steindl (16) pollen was found on the stigma, and, in some, pollen tubes were observed in the stylar tissue. Fertilisation had been expected to occur in all the species investigated.

Although the pollen tubes were not seen in *L. rubromarginatus* (perhaps due to technical difficulties) this does not exclude fertilisation of the egg by a male gamete. In one case a small black body resembling the male nucleus was seen inside the polar nucleus (fig. 3). This may indicate that double fertilisation does occur.

In a large number of medium-sized buds a few embryo sacs are found in the tissue surrounding the sporogenous cells (Plate XXI, fig. 19; em.s.). These embryo sacs having no connection with the sporogenous tissue, thus appear to result from somatic cells, although such enlarging cells were never seen

in the younger stages of the bud. If this is the case, development of the embryo sac is aposporous and we can thus explain the probable diploid chromosome number found in the endosperm (which results from the division of the large basal nucleus) and the proembryo in the absence of pollen tubes. Another explanation for the probable diploid chromosome

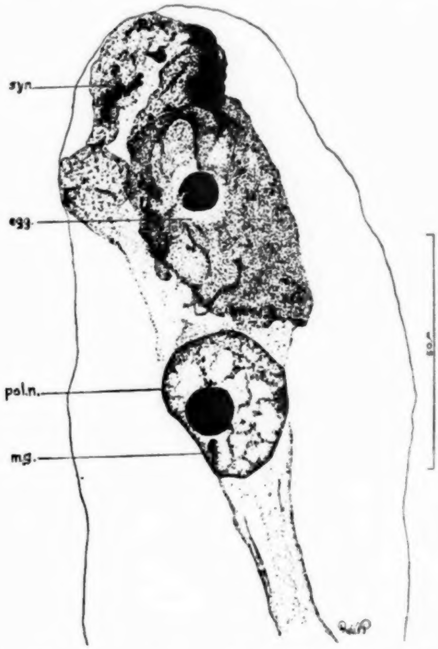

FIG. 3.—*Loranthus rubromarginatus*. A longitudinal section through the style, showing the apex of an embryo sac in which the synergids have degenerated. In the upper polar nucleus, lying near the nucleolus, is an elongated black staining body which may represent the nucleus of a male gamete (m.g.). (× 700.)

number in the endosperm (see below) may be put forward. The lower nucleus of the two-nucleate embryo sac might have undergone a division, the resulting nuclei then fusing to form the one large basal nucleus of the embryo sac. This fusion would then be analogous to the nuclear fusion in the *Fritillaria*-type embryo sac (10). However, this type of development is considered extremely unlikely, because never were two nuclei observed in the basal end of the embryo sac. The sporogenous cells (megaspores, etc.) in these medium-sized buds were in a degenerating condition and this is a further argument for apospory in *L. rubromarginatus*.

Thus, although megaspores and two-nucleate embryo sacs are formed as in the other Loranthoideae, the mature embryo sac may be an aposporous structure having the diploid chromosome number. Further experiments are to be conducted in order to elucidate this very important point.

VI. Early Embryogeny.

The first division of the egg, whether parthenogenetically or after fertilisation, is considered to be longitudinal after studying fig. 17 (Plate XXI), which illustrates a very early stage in embryonic development. Further proof is found in the genera *Taxillus* (16) and *Helixanthera* (12) where the fertilised egg has been seen to divide longitudinally into two. Using then the classification of Johansen (6), embryonic development of the Loranthoideae appears to be of the *Piperad*-type or a modification thereof. The proembryo at first consists only of suspensor cells, resulting from the transverse divisions of the first two cells (Plate XXI, fig. 17). At a slightly later stage the cells at the apex of the proembryo cut off two dome-shaped embryo cells. These embryo cells undergo no further division until a much later stage. Elongation of the suspensor, resulting in the downward push of the embryo along the tubular embryo sac into the endosperm, is due to the transverse divisions of the suspensor cells immediately behind the embryo. The suspensor cells, after attaining their full length, disintegrate (Plate XXI, fig. 18). The suspensor of *L. rubromarginatus* in some cases consists of two rows of cells (Plate XXI, fig. 17) and in other cases of four rows (Plate XXI, fig. 18). The suspensor of all the genera investigated by Schaeppi and Steindl, however, consists only of two rows of cells.

Soon after development of the egg the upper polar nucleus degenerates.

In the meantime, just after the egg starts dividing, the large basal nucleus of the embryo sac divides to form a number of cells with a dense cytoplasm which borders on the collenchymatous plate (Plate XXI, fig. 16). Above this cellular group, which much resembles the antipodals of the other angiosperms, there are one or more free nuclei (also the progeny of the large basal nucleus), one of which can be seen dividing in fig. 16 (Plate XXI). More than nine chromosomes could be counted at each pole of this anaphase, and as nine was found to be the haploid number the endosperm will probably be diploid. The antipodal-like cells are arranged in more or less regular rows. They enlarge and become vacuolated, cell-walls are formed between the few free nuclei, and all these cells, by further divisions, form the endosperm in the basal end of the embryo sac (Plate XXI, fig. 18). The endosperms of the various embryo sacs later unite to form a compound endosperm as is the case with *Helixanthera* (12).

A number of egg cells were found to develop, as had been observed for

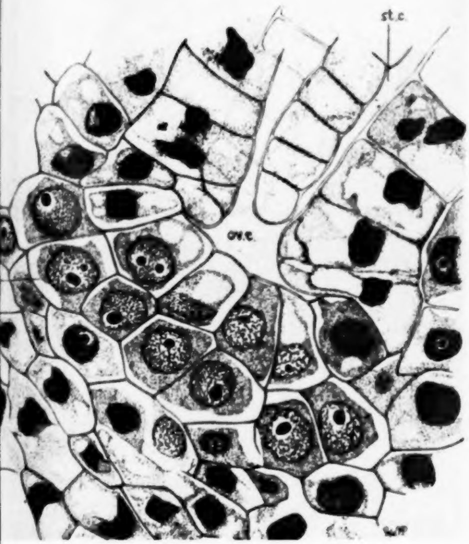

Fig. 4.

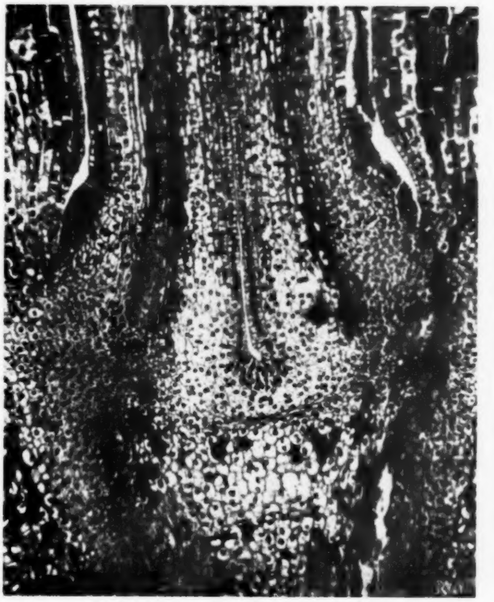
Fig. 5.

Fig. 6.

Fig. 7.

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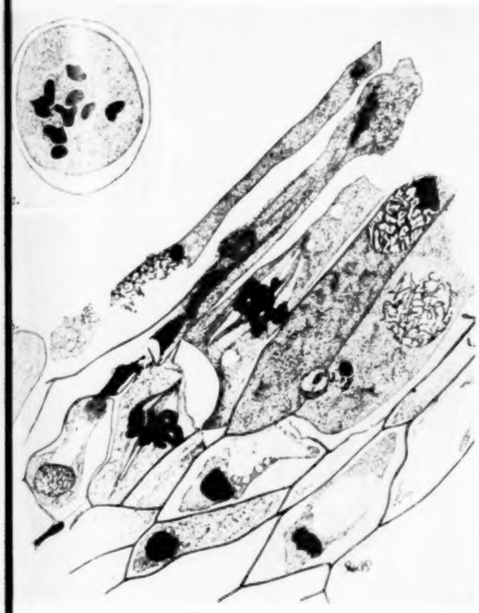

Fig. 8.

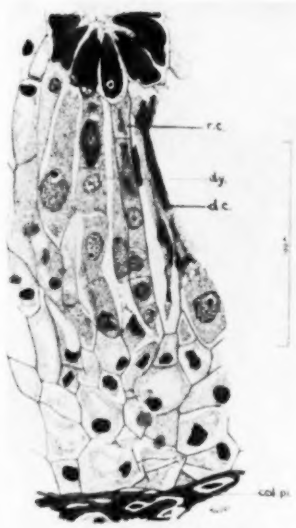

Fig. 9.

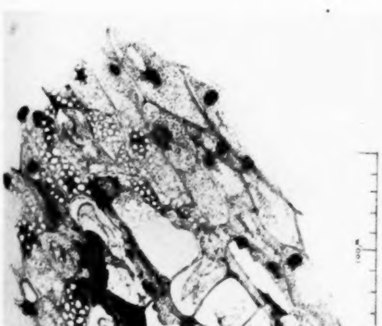

Fig. 10.

Fig. 11.

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FIG. 12.

FIG. 13.

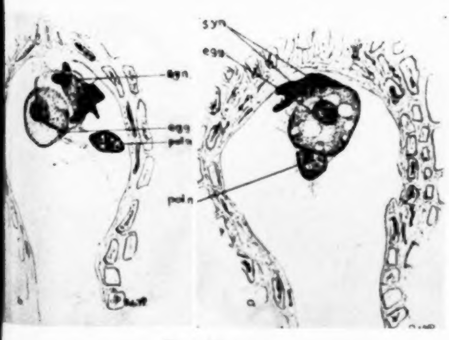

FIG. 14.

FIG. 15.

FIG. 16.

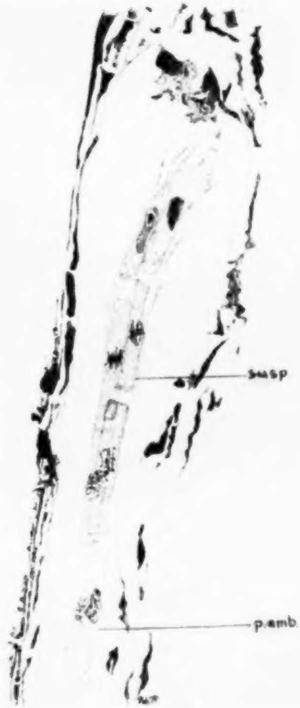

FIG. 17.

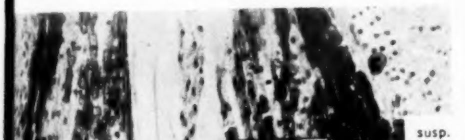

FIG. 18.

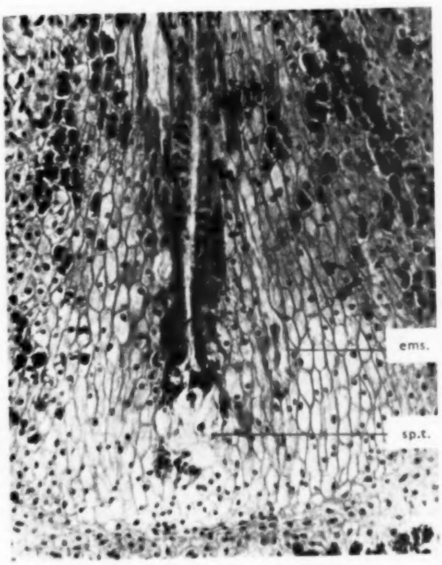

FIG. 19.

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other Loranthoideae, so that three or more suspensors with two-celled embryos were seen in the endosperm in the ovary. As a rule, however, only one of these forms the mature embryo of the fruit.

The fruit is a pseudo-berry, consisting of ovarian and receptacular tissue. When ripe, these fruits are about 1·8 cm. long and have a bright red skin. Below the skin is a slimy layer, inner to which is the sticky layer enveloping the endosperm in the centre. In the middle of the endosperm a large green embryo with two cotyledons is found. Marloth (13) found that the embryo of *Loranthus* "sometimes germinates before the fruit is removed from the branch." Birds serve as the agents of transmission.

VII. Discussion and Conclusions.

Except for the structure of the arrow-type tetrasporangiate stamens, the floral structure and its development in *Loranthus rubromarginatus* are very similar to that of the other Loranthoideae, especially *Dendrophthoe* and *Taxillus*, which also have the same floral formula, viz. ⚥ ○ $P\widehat{(5)}A5\overline{G}(5)$. *L. rubromarginatus* belongs to that Loranthoidean group in which no placenta is formed.

Microsporogenesis follows the rule of the normal dicotyledonous type. The haploid number of nine chromosomes is the same as that of *L. longiflorus* and *Amyema gravis.*

At the base of a small ovarian cavity a number of archesporial cells are formed hypodermally. These differentiate into the macrospore mother-cells after further elongation and one or more divisions. Thus, as Schaeppi and Steindl found in *Helixanthera hookeriana* and *Dendrophthoe,* and Maheshwari and Johri in *H. ligustrina*, a large number of megaspore mother-cells are formed, instead of the one or two as in the reduced ovules of *Lepeostegeres* and *Macrosolen.*

Megasporogenesis as in *Lepeostegeres gemmiflorus, Elythanthe parasitica,* and *Helixanthera hookeriana* (16) follows the "Normal-type." The megaspores were found to possess the reduced number of chromosomes.

After formation of the two-nucleate embryo sac, the embryo sac elongates rapidly forming a thin tube up the style. Downward growth is checked by the collenchymatous plate. Growth of the embryo sac is thus similar to that of the other Loranthoidean genera.

No four-nucleate embryo sac is formed as in *Lepeostegeres, Macrosolen* and *Helixanthera* (16), because the lower nucleus of the bi-nucleate sac remains undivided. A three-nucleate sac is thus formed instead. Both the upper nuclei of the three-nucleate sac probably divide, as was found by Maheshwari and Johri in *H. ligustrina*, thus resulting in a five-nucleate sac. These upper four nuclei in the apex of the embryo sac, which at this stage may be

found 35 mm. up the style, then differentiate into the egg apparatus and upper polar nucleus. The structure of the egg apparatus very closely resembles that of the other Loranthoideae studied by Maheshwari and Johri, and Schaeppi and Steindl, except that the latter authors found a secondary nucleus instead of an upper polar nucleus lying near the egg-cell. The lower nucleus in the base of the embryo sac remains undivided, unlike most other genera, and the mature embryo sac is thus five-nucleate. Therefore, as in most other investigated species, no antipodals, as found in *Scurrula atropurpurea* (16), are differentiated.

Up to nine embryo-sac apices were found in the style of *L. rubromarginatus*, but as many as twelve have been found in the style of *Dendrophthoe.*

Phylogenetically, *L. rubromarginatus* is probably one of the most advanced genera of the Loranthoideae, not only because of the extreme simplification in the ovary as in *Dendrophthoe* and *Scurrula* (16) but also because of the enormous elongation of the embryo sac which, although not reaching the stigma as in *Helixanthera* (12, 16), is very much longer than the embryo sac of the latter genus.

Loranthus rubromarginatus is suspected to be apomictic. Not only were no pollen tubes observable, but the ovarian sporogenous cells also appeared to be in a degenerating condition. Further argument for this assumption is found in the medium-sized buds where embryo sacs are found in the tissue surrounding the sporogenous cells. The embryo sac developing from a somatic cell would thus be diploid. A division of a free nucleus during endosperm formation indicated the probable diploid nature of the endosperm. The endosperm was, however, formed from divisions of the large lower embryo sac nucleus. As no nuclear fusions were observed in the basal end of the embryo sac this might suggest a diploid nature for the embryo sac.

The first division of the egg is thought to be longitudinal, as was found in *H. ligustrina* (12) and *Taxillus* (16). Embryo development is thus of the *Piperad* type. A long suspensor, which may consist of two or four rows of cells, pushes the two-celled embryo down the style into the endosperm. As in other investigated species, a number of embryos may be pushed into the endosperm, of which only one as a rule will mature.

The endosperm in the species investigated by Schaeppi and Steindl was found to develop from a fusion nucleus. In *L. rubromarginatus* the endosperm, however, is formed from the large basal nucleus. The first formed endosperm cells, which are formed just after proembryo development starts, very much resemble the multicellular antipodals of other angiosperm embryo sacs. Thus, although the so-called endosperm in *L. rubromarginatus* in structure and function resembles the true endosperm of the other investigated species which is formed from the triple-fusion nucleus (16), there

can be no homology since it develops from the unrelated basal nucleus of the embryo sac. This nucleus is not equivalent to the lower polar nucleus, because it is still two generations earlier in development, being the lower nucleus of the two-nucleate embryo sac. The endosperm in *L. rubromarginatus* is therefore more homologous to the antipodals of the other angiosperm embryo sacs than to a true endosperm, although its formation only commences after the proembryo starts to develop. However, because this tissue, as said, in form and function resembles an endosperm, I prefer to call it "endosperm" rather than an "antipodal tissue."

Acknowledgments.

I here wish to express my indebtedness to Dr. S. Krupko for suggesting the problem, for his kind supervision, helpful suggestions, and for some of the collected material.

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EXPLANATION OF PLATES.

Plate XVIII.

Fig. 4. A longitudinal section through the ovary of a small bud (fig. 2, *d*), showing the hypodermal archesporial cells (ar.c.) at the base of the ovarian cavity (ov.c.). st.c., stylar canal. (× 710.)

Fig. 5. A longitudinal section through an 8-mm.-long bud, showing the hypodermal archesporial cells which become elongated. (× 81.)

Fig. 6. A longitudinal section through the ovary of a bud slightly older than the one illustrated in the previous figure, showing the loosely arranged archesporial cells (ar.c.). (× 390.)

Fig. 7. *a*, Megaspore mother-cells (mg.m.c.) lying hypodermally at the base of the ovarian cavity as seen in a longitudinal section through a 34-mm.-long bud. *b*, Nucleus of the fourth cells from the left in (*a*) in the pachytene stage. *c*, Nuclei of the cells on extreme right in (*a*); the upper damaged nucleus is in the diplotene stage and the lower is in the leptotene stage. (*a*, × 310; *b*, × 950; *c*, × 710.)

Plate XIX.

Fig. 8. *a*, Polar view of first meiotic metaphase in a pollen mother-cell. *b*, A longitudinal section through a 34-mm.-long bud, showing the first meiotic metaphase in two megaspore mother-cells. (× 690.)

Fig. 9. A longitudinal section through a 34-mm.-long bud, showing two groups of dyads (dy.), the one above the other. Megaspore mother-cells on right degenerating, others still have nuclei in first meiotic prophase. col.pl., collenchymatous plate. (× 310.)

Fig. 10. A longitudinal section through a medium-sized bud, showing linear tetrads of megaspores. (× 310.)

Fig. 11. A longitudinal section through the ovary of a medium-sized bud, showing two bi-nucleate embryo sacs from the upper megaspores of two linear tetrads. The other sporogenous cells are degenerating. t.em.s., two-nucleate embryo sac. (× 300.)

PLATE XX.

Fig. 12. A longitudinal section through the ovarian region of an open flower, showing the basal regions of three mature embryo sacs, the centre one revealing the single lower nucleus which is found in the base of every embryo sac. (× 92.)

Fig. 13. A longitudinal section through the style of an open flower, showing the club-shaped apex of an embryo sac containing a single nucleus (n.1). A second nucleus (n.2) is found in the embryo-sac tube 120 μ below the nucleus in the apex. These are the two upper nuclei of the three-nucleate embryo sac. (× 310.)

Fig. 14, *a*, *b*; Fig. 15. The apices of the embryo sacs which are found 22 to 35 mm. up the style. egg., egg cell; pol.n., polar nucleus; syn., synergids. (Fig. 14, *a*, *b*, × 158; Fig. 15, × 85.)

PLATE XXI.

Fig. 16. *a*, A longitudinal section through the ovarian region of an open flower, showing the base of a fertilised embryo sac. The lower nucleus (shown in fig. 12) has divided to give rise to 16 antipodal-like endosperm cells (end.) and three free nuclei, one of which is shown in this section in the late anaphase stage of mitotic division. *b*, The late anaphase stage of the mitotic division of the free nucleus in (*a*) more enlarged. From this division it appears that the diploid chromosome number is present in the endosperm. (*a*, × 310; *b*, × 710.)

Fig. 17. A longitudinal section through the style of an open flower, showing the apex of an embryo sac containing a young proembryo, consisting of six cells arranged in two rows. p.emb., proembryo; susp., suspensor. (× 255.)

Fig. 18. A longitudinal section through the ovary of an open flower, showing the large thin-walled endosperm in the base of the embryo sac and a suspensor pushing a two-celled embryo into the endosperm. (× 85.)

Fig. 19. A longitudinal section through the ovary of a medium-sized bud, showing an embryo sac (em.s.) towards the right which appears to have originated independently from the sporogenous tissue (sp.t.) at the base of the ovarian cavity. (× 104.)

THE MICROSCOPICAL EXAMINATION OF PLANKTON COLLECTIONS WHILE AT SEA.

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Planktologist to the Division of Fisheries, Cape Town.

(With two Text-figures.)

(Read October 18, 1950.)

Introduction.

The microscopic examination of plankton on shipboard, even with the lowest power objectives, has always proved something of a problem, inasmuch as even in the calmest weather there is always a certain amount of movement of the vessel.

A delicately balanced gimbal table does, to a certain extent, steady the fluid in which the plankton is preserved, but it does not completely arrest movement, especially in rough weather.

In an extensive research programme involving large numbers of collections it is particularly desirable that at least some preliminary examination should be made on board, otherwise all material must be taken to the shore laboratory at the end of each cruise, and if the collections are many in number it will be found almost impossible to work them up before the ship is again ready for sea. This leads, over a period of months, to a building up of a large mass of material on shore—a most disheartening state of affairs, discouraging careful study and producing a temptation to hurry the work, which in turn produces sketchy, or even false results.

A method has, however, been evolved by which an entire plankton collection can be examined even in rough weather, under low and high or medium powers, both quantitatively and qualitatively with a very fair degree of accuracy, and since it may be of some interest to marine biologists generally, a short description is given in the following pages.

Principle of the Apparatus.

The method employed consists solely of an adaptation of the simple siphon. Fig. 1 shows the general features and fig. 2 a photograph of the apparatus in experimental form.

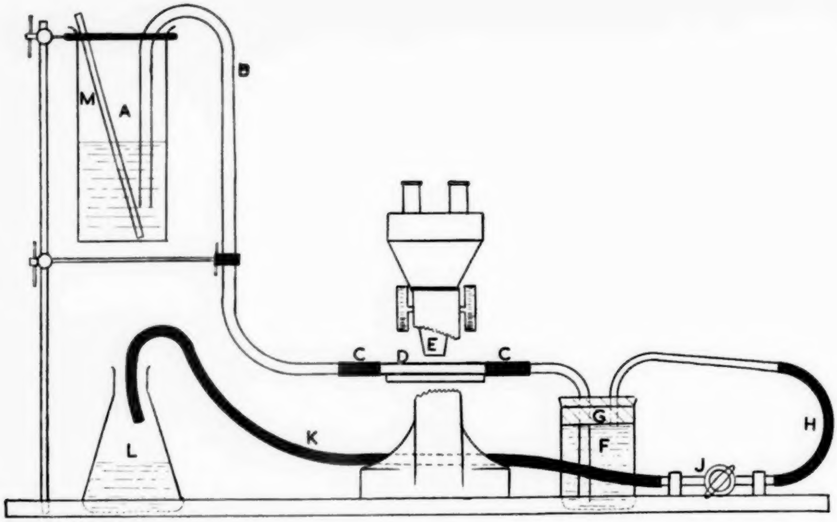


Fig. 1.

(Explanation.)

A. Container for collection.
B. Half-inch glass siphon tube.
C. Rubber-tube connections.
D. Square tube made of perspex.
E. Objective of microscope.
F. Closed trap for re-collecting plankton.
G. Tight-fitting rubber stopper.
H. Second part of siphon connected to control tap.
J. Glass two-way control tap.
K. Rubber delivery tube completing siphon.
L. Collecting flask for water.
M. Solid glass stirring rod.

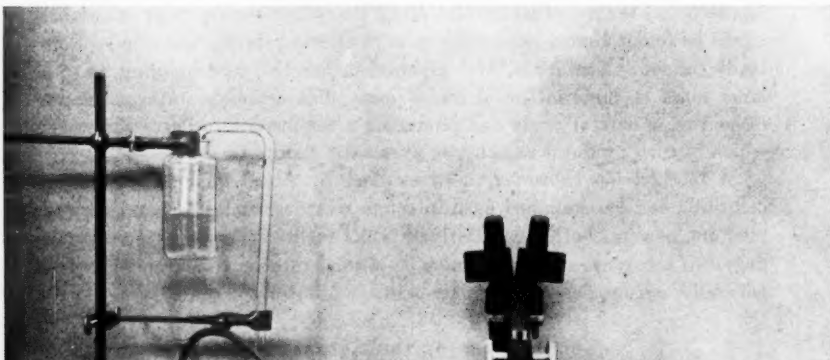


Fig. 2.—Photograph of the experimental apparatus.

The open container (A) to receive the fluid containing the collection is placed on the left of the operator and clamped firmly some eighteen inches above the bench. From this a half-inch diameter siphon tube (B), its receiving end about two inches above the container bottom, is curved gently over to descend vertically to a point some six inches below the bottom of the container, and then curved gently to the horizontal, on a level with the stage of the microscope to be used. It is then connected by rubber tubing (C) to a square section tube 8 mm. × 6 mm. internal measurement (D), which just fills the field of the low power objective (E) in this particular case, but which can be made to any desired size. (See description of how the square tube was made later.)

The square tube rests on the microscope stage and is connected to a glass tube which curves downwards to within half an inch of the bottom of a delivery trap (F) through a rubber cork (G). Another glass tube, let in flush with the lower surface of the rubber cork, takes liquid *only* further along the siphon (H) leaving the plankton at the bottom of the delivery trap. An ordinary two-way tap (J) is inserted in the flow so that the flow can be controlled in pace or stopped instantly at will. The siphon is completed to the open flask (L) below the original container. Liquid from this flask is poured back from time to time into the container to top up the level of fluid, and thus avoid running the siphon "dry".

The siphon system is now filled with water, and the plankton collection, from which the larger organisms have been extracted, poured into the container. This is stirred with a glass rod (M) and the siphon turned on while the organisms are in suspension. These can be seen coming over, and as soon as they approach the square tube the siphon is checked. In the container, organisms sink to *below* the siphon entrance, and the slow action of fluid as those in the tube pass under the microscope is not enough to draw any further plankton up until the "batch" has passed under the microscope. Stirring is repeated and a fresh supply drawn into the system.

The organisms can be made to pass at any desired speed, or stopped instantly for examination. Since the width of the square tube is exactly the diameter of the field, *all the organisms in the sample must come under scrutiny.* Moderate and even high power may be employed while the siphon is stopped, *and no movement of any consequence takes place in the square tube whatever the angle of the ship within* 25 *to* 30 *degrees*, if the apparatus is mounted "fore and aft" not athwartships. Qualitative and quantitative examination of as large a sample as necessary of that particular collection can therefore be made with great accuracy.

The Square Tube.

The obtaining of rectangular section glass tube presented great difficulty until the possibility of using *perspex* was suggested. By the use of a good cement and very fine emery cloth for squaring edges a good tube was soon produced, the scratches on the surface being eliminated by the use of ordinary metal polish and much patience. The ends were tapered off to prevent organisms getting lodged. The best thickness of perspex for this work was found to be one-eighth inch; and the tube made long enough to overlap each side of the staging by at least an inch, so that the rubber tubing connections could be made.

The refractive index of perspex being as low as 1·11, there is little interference, and if enough patience is used in polishing, the tube will be found optically satisfactory. In making the tube great care must be taken to avoid getting excess cement on the *inside*, as this cannot afterwards be removed. Excess on the *outside* does not matter as this can be removed with emery cloth and repolished to perfect transparency.

Limitations of the Apparatus.

Very few methods can claim perfection and the apparatus above described is no exception to the rule. In the first place, the collection must be "prepared"—objects of 5 mm. and over will not readily pass—and this will include such forms as Medusae and Salps and Ctenophores. Nevertheless, the trouble is worth while, and in the case of collections with the finer nets the amount of preliminary sorting out is small, while in many cases such as rich copepod collections, which are the most important, none at all is necessary.

Another drawback is that any rare object cannot be picked out—but an extension of the apparatus could be made so that any such object could be run off into a separate trap by having a junction piece to divide the exit flow, and controlled by a separate tap.

It is certain that many improvements and adaptations to suit varying requirements can be thought out and applied as necessity dictates, and so only the original idea has been set out in the hope that it may be of service to those whose interest in marine biology is such that ability to make even a cursory examination of plankton while still at sea will facilitate their work and relieve a shore staff of no small burden of arduous and, too often, irksome routine work.

THE STRUCTURAL FEATURES AND INCLUSIONS OF THE CAPE PENINSULA GRANITE.

By C. Boocock.

(With Plates XXII–XXIV and seven Text-figures.)

(Read March 15, 1950.)

Abstract.

The coarsely porphyritic biotite-granite of the Cape pluton, intrusive into the steeply dipping Malmesbury Series, extends the full length of the Peninsula. Structural features are feebly developed, primary flow structures being absent. The most prominent joint directions strike WNW.-ESE. parallel to the direction of stretching. They have been classified as longitudinal joints. Transverse NNW.-SSE. and NNE.-SSW. trending fractures are regarded as cross-joint directions. Secondary structures are undoubtedly present, but the primary age of these fracture systems is established by the fact that aplites follow them.

The Malmesbury Series in this area consists of psammitic strata with thinner pelitic intercalations. Both arenaceous and argillaceous strata have been converted into hornfels in the neighbourhood of the granite. Xenoliths of the Malmesbury sediments included in the granite show every gradation between normal hornfels and completely granitized fine-grained leucocratic granitoid rocks. Biotite-rich microgranitic xenoliths represent an intermediate stage.

In the initial stage of alteration the hornfels xenoliths were slightly enriched in alumina and cafemic constituents. This was followed by granitization effected chiefly by the introduction of potash-rich alkali material from the magma. Complete assimilation of downstoped sediments is believed to have modified the granite by causing an increase in the amount of biotite. The presence of cordierite in the granite is also ascribed to contamination.

The large microcline microperthite phenocrysts are considered to be the normal products of magmatic crystallization and not the result of late potash enrichment with the growth of replacement microcline.

CONTENTS.

I. Introduction.

(a) *Location and Extent of Outcrops of Granite.*—The Cape Peninsula extends from north to south a distance of about thirty-three miles and is an average of five miles in width, although it attains in one part a maximum width of ten miles. Most of the high ground is formed of a thick series of quartzitic sandstones folded in a gentle syncline with a NW. to SE. axis.

The coarsely porphyritic biotite granite of the Cape Peninsula pluton, intrusive into steeply dipping pre-Devonian Malmesbury sediments, forms the peneplain on which the quartzites of the Table Mountain Sandstone Series rest with marked unconformity. These quartzites produce steep coastal cliffs where faults have carried the granite basement below sea-level. Outcrops of sediments of the Malmesbury Series are confined to the northern portion of the Peninsula (fig. 1), while the shores and talus-covered slopes from Sea Point to Ratel Klip, at the northern end of Chapmans Bay, consist of granite. The granite does not appear at any point south of this on the west coast. On the east coast the granite forms the shore and lower mountain slopes from Simonstown to Smitswinkel Bay, outcropping finally at the southern extremity of the peninsula at Cape Point. A granite outcrop trending east-west similarly forms the shore-line on the southern side of Fish Hoek Bay. Further small outcrops occur on the Cape Flats near Zeekoe Vlei. The large granite area on the eastern slopes of Table Mountain is densely wooded or built over, and in so weathered a condition as to render study of it impracticable.

(b) *Previous Work.*—The granite has been studied in part by several

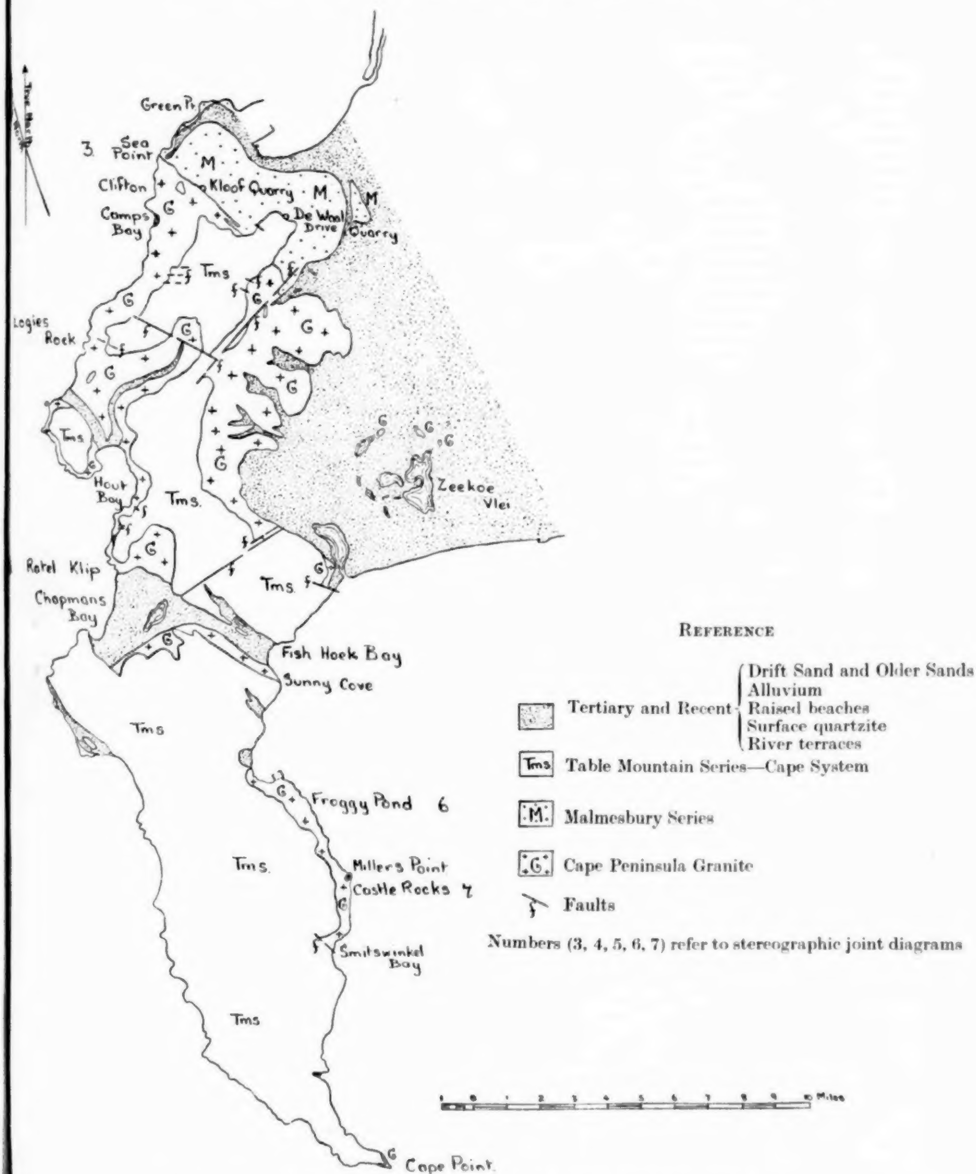


FIG. 1.—Generalized geological outcrop map of the Cape Peninsula pluton.

workers since the famous granite-Malmesbury contact was first recorded in 1813 (Hall) and 1818 (Abel). Most recent accounts have been given by E. H. L. Schwarz (1913), A. R. E. Walker (1929), D. L. Scholtz (1947), and F. Walker and M. Mathias (1947).

Schwarz described the Sea Point contact area and concluded from the evidence exposed there that "the granite, far in from the contact, shows that it has originated by the replacement of slate. . . ."

A. R. E. Walker summarized the main field characters of the contact area.

Scholtz undertook an exhaustive and detailed investigation of the younger pre-Cambrian granite plutons of the Cape Province and arrived at the general conclusion that the granite was primarily the result of gravitational differentiation combined with minor contamination.

Walker and Mathias confined their investigations mainly to the contact phenomena and gave their explanation of these and of the granite genesis. They concluded that the intrusion of a "contaminated biotite-granite magma" was followed by "permeation and softening of the Malmesbury hornfelses by alkaline emanations from the granite". Further stages in the development of the contact phenomena were considered to be "permeation of the hornfelses by granitic material with the formation of migmatites", and finally "felspathization of the granite and migmatite zone by late potassic solutions which gave rise to potash pegmatites and large crystals of perthitic microcline". Evidence for the formation of an MgFe front outside the migmatite zone was found to be inconclusive. The paper provides fourteen new analyses, and these chemical data have been extensively utilized in the study of the geochemical changes leading to granitization of the Malmesbury sediments in the granite.

The present investigation was carried out in an attempt to discover the form and method of emplacement of the pluton and to determine the petrographic nature of the inclusions of Malmesbury sediments within the granite.

II. Texture and Mineralogical Composition of the Peninsula Granite.

Quantitative petrological data concerning the Peninsula granite have been given by M. Mathias (1940, pp. 197–199), C. B. Coetzee (1941, pp. 196–202), D. L. Scholtz (1947, pp. xlvii–xlviii and lviii–lxii), and by F. Walker and M. Mathias (1947, pp. 502–506). Only a brief summary of the main features is included.

(a) *Texture.*—Texturally coarsely porphyritic biotite-granite of exceedingly uniform composition predominates. The grain size of the matrix is about 3 mm., while phenocrysts of potash felspar average 4 cm.

A fine-grained porphyritic granite of rather irregular distribution and small extent occurs at Sea Point and Kloof quarry, showing phenocrysts up to 2 cm. in length set in a matrix in which the average grain size is 0·3 mm. It passes gradationally into the normal porphyritic granite.

An even-grained modification of the normal Peninsula granite occurs on the shore below Sunny Cove station.

Aplites with an equigranular texture and grain size generally less than 1 mm. are abundant in the granite. Just outside the migmatite zone at Sea Point is a thick mass of aplogranite which shows a close textural resemblance to the aplites.

(b) *Mineralogical Composition.*—The Peninsula granite is a grey biotite-granite containing phenocrysts of microcline microperthite in a medium even-grained base of quartz, microperthite, oligoclase, and biotite. Phenocrysts of microcline microperthite are white and usually twinned according to the Carlsbad law. The phenocrysts are generally subhedral and are seen to include numerous crystals of quartz, biotite and plagioclase. Potash felspar of the matrix is also microperthitic with a small amount of microcline microperthite.

Plagioclase crystals are always colourless or white with the composition of oligoclase (An_{25}). The plagioclase of the fine-grained porphyritic granite is more sodic with An_{10}. Slight alteration to kaolin, saussurite or muscovite is evident.

Quartz occurs as irregular crystals averaging 1·3 mm. in diameter. They often show evidence of strain.

The dominant ferromagnesian mineral is biotite with intense pleochroic haloes about included zircons. Pleochroism is marked and generally from X = pale yellow-brown to Y and Z = reddish brown. Alteration is to chlorite or occasionally to muscovite, the alteration sometimes being accompanied by the exsolution of sagenite and the separation of iron ore. A minor amount of muscovite is generally present, but little, if any, appears to be of primary origin. Rectangular cordierite crystals up to 2 cm. in length, mainly altered to pinite, are a characteristic feature. Both the biotite and cordierite tend to occur in clots.

Tourmaline is of widespread occurrence, being particularly abundant in the granite at Millers Point and in the even-grained modification at Fish Hoek. Yellow or brown varieties predominate and tourmaline preferentially attacks perthite and biotite.

Accessory minerals include apatite, magnetite, zircon, pyrite and more rarely almandine garnet and xenotime. The even-grained modification at Sunny Cove contains a small proportion of green hornblende though it has a patchy distribution. Scholtz (1946, p. lxi) records andalusite from Fish Hoek.

The mineralogical composition of other textural types does not differ greatly from that of the normal granite. In the fine-grained porphyritic granite, muscovite is more abundant than biotite, and brown tourmaline becomes a fairly important constituent. The aplitic veins are the exact counterpart mineralogically and texturally of the matrix of the fine-grained porphyritic granite except for a poverty in cordierite (Walker and Mathias, 1947, p. 505). The aplogranite closely resembles the fine-grained aplites, but it contains little or no biotite.

Veins and nests of pegmatite, which are fairly common in the granite, often show radiating bunches of tourmaline needles. They consist of quartz, coarsely perthitic microcline and muscovite, with or without biotite and tourmaline. Aplite veins frequently pass marginally or centrally into thin pegmatites. Coarse granitic or pegmatitic facies are common, surrounding small, rounded hornfels inclusions.

Xenoliths of Malmesbury sediments in various stages of alteration are found throughout the normal porphyritic biotite granite and fine-grained porphyritic granite, though they are absent from the even-grained modification of the Peninsula granite on the south side of Fish Hoek Bay.

III. The Malmesbury Series.

The contact between the steeply dipping and isoclinally folded pre-Devonian Malmesbury Series and the Peninsula granite strikes roughly NW.–SE. Exposures are revealed at Platteklip Gorge on Table Mountain, at Kloof quarry and at Sea Point. At the latter two places the contact is a concordant one, and at Sea Point a migmatite zone 70–80 yards in width separates the granite and the hornfelsed sediments. The migmatites have been described in detail by Walker and Mathias (1947, p. 507). The mixed rocks, which have a wavy and streaky appearance, consist of an intimate mingling of granite and slate containing porphyroblasts of potash felspar which resemble the phenocrysts in the granite.

The Malmesbury Series in this area consists of fine-grained arenaceous strata with thin, slaty intercalations. The abundant arenaceous layers are best described as "fine-grained argillaceous arkoses or siltstones" (Walker and Mathias, 1947, p. 506), being composed mainly of clastic angular grains of quartz (average grain size 0·1 mm.) with a considerable proportion of sodic oligoclase (An_{12}) and some minor microcline, both felspars being comparatively fresh. The groundmass consists of biotite and sericite with only slight parallelism. In places, circulating solutions have altered the biotite to chlorite. The pelitic strata have much finer grain size. They show very rapid alternations of composition, but consist essentially of biotite and sericitic mica showing well-marked parallelism with quartz

and minor sodic oligoclase and microcline. Clay minerals are also present.

The ubiquitous occurrence of biotite in the sediments is due to low-grade regional metamorphism which affected the Malmesbury Series prior to the intrusion of the granite.

Types of intermediate chemical and mineralogical composition between the argillites and siltstones are common.

Both argillaceous and arenaceous strata have been converted into hornfels in the neighbourhood of the granite. In the contact aureole the sediments are seamed with veins of quartz, aplite and pegmatite; while spotting, due to the development of poikiloblastic cordierite, is prominent in both pelitic and semipelitic rock types. The cordierite areas measure 1–5 mm. across and contain abundant inclusions of biotite and quartz. Close to the contact the spotting becomes less conspicuous, the cordierite being relatively free from inclusions, while the hornfelses become more coarsely crystalline and lose their clastic appearance.

IV. Structural Features of the Cape Peninsula Granite.

(a) *Weathering.*—The granite shows a tendency to occur as large exfoliated dome-like masses or as massive rounded boulders of very variable dimension accumulating on the talus-covered slopes below the cliffs of the Table Mountain Sandstone Series or on the shore above high-tide level.

At Camps Bay peculiar sculpturing effects have been produced on the south-eastern side of the outcrops by wind-blown sand grains (Plate XXII, photo 1). Pitting is produced on vertical faces, while inclined surfaces are grooved. Polishing of the naked outcrops, which is most markedly developed on the northern side of Camps Bay beach, occurs right round to Bachelors Cove. To the south, similar weathering effects have been produced on the granite of Ratel Klip on the north side of Chapmans Bay.

South of Simonstown, near Millers Point, selective erosion along intersecting joint systems in the intertidal portions of the coast has produced areas studded with oriented depressions averaging a foot in diameter (Scholtz, 1946, p. xlix).

As a result of their more rapid disintegration, dolerite dykes tend to form furrow-like depressions in the enclosing granite.

Due to their greater resistance, xenoliths, particularly those rich in ferromagnesian minerals and quartz, often stand in relief as brown or black wart-like nodules.

(b) *Structural Features.*—One hundred joint directions were measured at each of five different localities in the Cape Peninsula (fig. 1) corrected for magnetic declination and plotted stereographically (figs. 2–6).

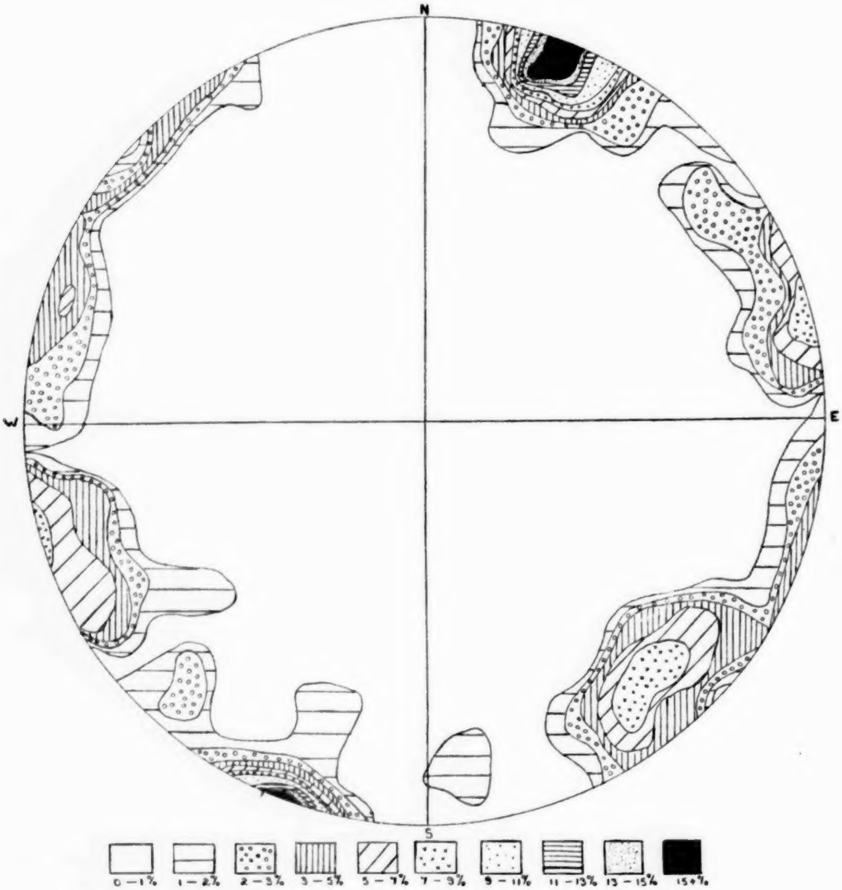


FIG. 2.—Stereographic projections of 100 joint directions mapped at Sea Point area.

From the joint diagrams it can be seen that the maxima show marked agreement in all areas, with the most prominent joint directions in the Cape Peninsula pluton striking WNW.-ESE. (From N. 87 W. to S. 87 E. and N. 65 W. to S. 65 E.) This is not only true of the selected area, but throughout the pluton WNW.-ESE. is the major and most prominent direction. At Cape Point the main joint directions strike E.-W. rather than WNW.-ESE. The joint diagram of the Froggy Pond area shows an additional maximum striking N. 23 E.-S. 23 W. Joints striking in a general NNW.-SSE. direction are also prominently developed in the pluton.

The stereographic diagrams indicate that the majority of joints have a steep dip. The relative paucity of joints with low dip is partly due to the difficulty of differentiating between exfoliation phenomena and flat-lying joints. Further, the mapping of joints was confined to the coastal areas as giving the best exposures, and erosion tends to follow such directions, rendering accurate measurements difficult.

Aplites are abundant throughout the granite. They do not generally exceed 2 feet across, commonly showing a ramifying and transgressive tendency. Several aplites, however, range up to 50 feet across, particularly south of Simonstown on the False Bay coast and display a distinct tendency for preferred orientation NNE.-SSW., and NE.-SW. with WNW.-ESE. being of subsidiary importance. At Millers Point two distinct sets of aplite veins, striking WNW.-ESE. and NE.-SW., cut the granite. There is no evidence to indicate that they are not contemporaneous. Quartz veins trend WNW.-ESE. and NE.-SW., the former direction being the more important.

The contact between the invaded Malmesbury Series and the granite is a concordant one striking in a general NW.-SE. direction. Near the contact the dip of the sediments is very nearly vertical, but slightly to the north, near Green Point, it is about 45 degrees. The clear-cut contact between the granite and migmatite and the evidence of the penetration, softening and stoping of the Malmesbury sediments all indicate intrusive relationships, and the granite is considered to have been intruded in a mobile condition. The Cape Peninsula pluton has the characters of a "subsequent" batholith (*cf.* Sullivan, 1948, p. 489).

Primary flow structures, however, were not observed in the pluton, and this factor, combined with relative lack of knowledge of the structure and tectonic history of the Malmesbury Series in the South Western Cape, makes any attempt to discover the form and structure of the Cape Peninsula pluton extremely difficult. Little can be added to the conclusions of Scholtz (1947) concerning the structure of the plutons of the Cape Province.

The south-western plutons all appear to be markedly elongated parallel

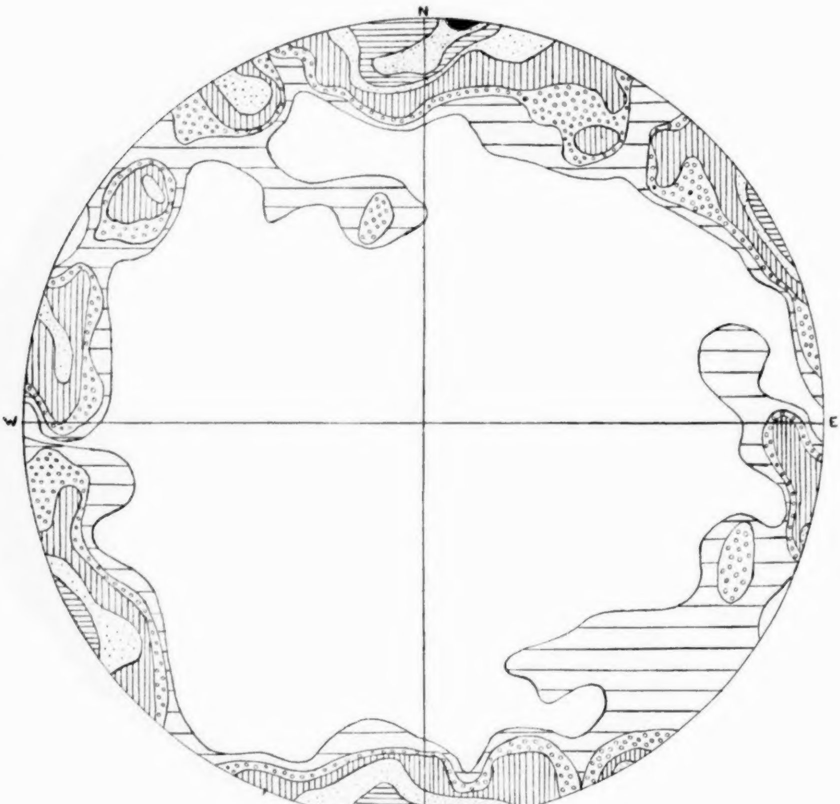


FIG. 3.—Stereographic projections of 100 joint directions mapped at Logies Bay area.

to a NW.-SE. direction, and in the Cape pluton there appears to be a preferred orientation along the frequent joints striking WNW.-ESE.

On this basis the joints can be tentatively classified according to Balk (1937). The prominent joints striking WNW.-ESE. parallel to the direction of stretching become longitudinal joints, while the transverse NNW.-SSE. and NNE.-SSW. trending fractures may be regarded as cross-joint directions. The majority of the aplites thus follow the cross-joint directions. This is in keeping with the conclusions of Balk, who states that cross joints are entirely of primary age whereas longitudinal joints may be of primary and secondary age.

Before the deposition of the T.M.S. the Malmesbury Series underwent severe folding along axes striking roughly WNW., frequently with the production of isoclinal folds, which invariably dip at high angles. As a general conclusion, embracing the structural features of all the plutons of the Cape Province, Scholtz (1947, p. lxxx) states that "the regional trend of the tectonic axes of the invaded rocks, the relations which the intrusives bear to their wall rock, as well as the primary and secondary structures exhibited by them, seem to indicate that they were emplaced towards the close of the Malmesbury orogenic cycle under the waning compressive stress acting from the WSW. or SW."

The direction of elongation of the Cape pluton parallels the general and dominant trend of the regional axes of the Malmesbury. While the structural relationships are largely obscured, available evidence seems to indicate that the granite rose concordantly along the heart of an anticlinal fold in the Malmesbury Series, a conclusion reached by Scholtz (1947, p. lxxx) and Walker and Mathias (1947, p. 509).

Consolidation of the igneous mass was followed by the development of the primary fracture systems and injection of aplite dykes and veins along dominant NE.-SW. directions. The cross-cutting aplogranite outside the migmatite zone at Sea Point and the even-grained modification at Fish Hoek show remarkable resemblances to the fine-grained aplites and they are considered to be younger than the main mass of porphyritic biotite-granite. Finally, differentiation, with the formation of felsic derivatives, led to the segregation of aplite veins and nests of pegmatite, the former showing a ramifying and transgressive tendency in the granite.

There is little evidence of forceful injection of the granite, which has not appreciably disturbed the general regional structure of the Malmesbury sediments. Contact phenomena indicate that the granitic material rose along the larger ruptures in the sediments and stoped off large blocks of the country rock. Evidence that stoping and fragmentation of rafts of sediments must have played some part in the emplacement process is afforded by the large xenoliths near the contact and the scattered smaller rounded

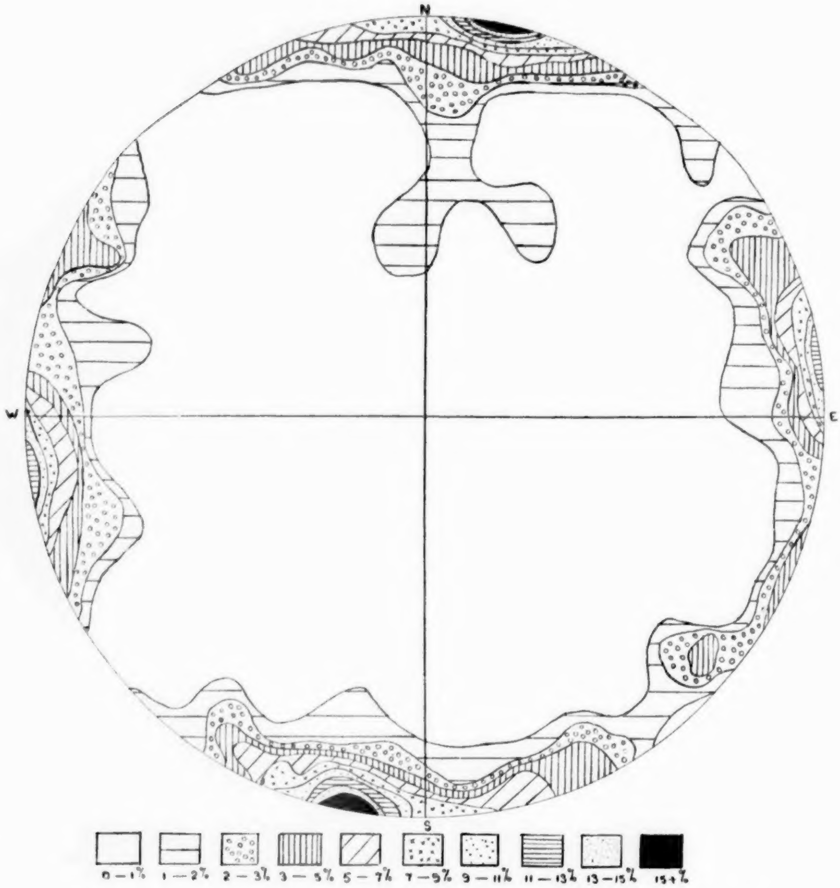


FIG. 4.—Stereographic projections of 100 joint directions mapped at Ratel Klip area.

inclusions found on all exposures of the normal porphyritic granite. To account for their relatively uniform distribution there must have been a certain amount of movement in the magma, though in the main this must have taken place before the inclusions were much softened by reaction. Their general rounded, spherical or more angular form indicates that little movement occurred after they were rendered plastic. The fact that the granite magma was capable of softening the Malmesbury hornfelses and evidence that they were rendered plastic is provided by the ptygmatically folded quartz veins in the migmatite zone (Schwarz, 1914, p. 37).

V. Malmesbury Xenoliths in the Granite.

Xenoliths of Malmesbury sediments in all stages of incorporation are widely distributed throughout the coarsely porphyritic Peninsula granite. The larger masses are confined to the contacts, smaller rounded xenoliths being more common farther from the junction. The inclusions generally end abruptly against the granite, and an intermediate or transitional zone is absent. On occasion the hornfels type of inclusion is surrounded by coarse granitic or pegmatitic segregations. Where reaction with the magma has been more intense, wisps of biotite-rich schlieren in the centre of coarse pegmatitic facies or shadow xenoliths of biotite-rich schlieren alternating with biotite-poor layers are the only evidence of the former presence of inclusions. Certain of the xenoliths have been veined by the enclosing granite, while in others pockets of quartz crystals are present.

While the number of inclusions is fairly uniform throughout the granite there is considerable local variation in abundance. In places, particularly from south of Hout Bay to Chapmans Bay, there are patches embracing a few square yards where the included material may make up as much as 20 to 30 per cent. of the surface area of the rock, while at other places inclusions may be almost wanting. The occurrence of xenoliths in local concentrations has led Scholtz (1947) to suggest that these swarms represent the local disruption of a much larger inclusion.

The xenoliths show no anomalous features other than the variation in spatial relations. Similar types of xenoliths are found on all exposures.

The inclusions found on the Atlantic coastal exposures differ neither megascopically nor microscopically from those on the False Bay coast. The similarities are also consistent in those xenoliths found on the Cape Flats exposures.

For descriptive purposes the xenoliths can be conveniently and broadly classified into two groups—hornfels inclusions and granitic inclusions, the latter representing the completely granitized product of the Malmesbury sediments.

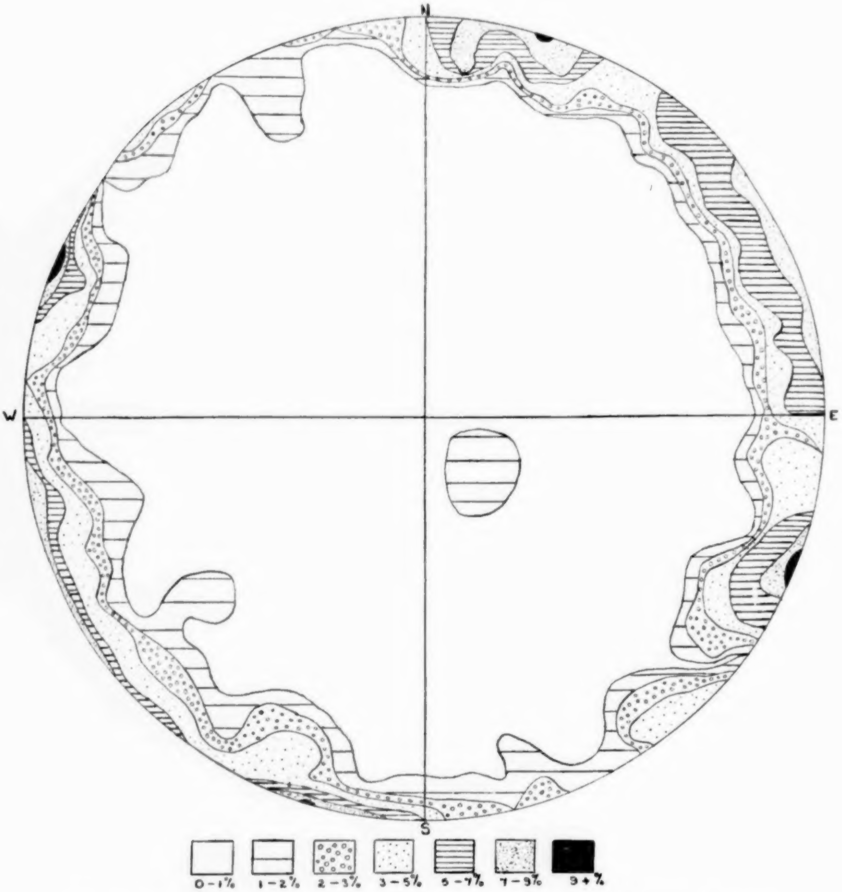


FIG. 5.—Stereographic projections of 100 joint directions mapped at Froggy Pond area.

(a) *Hornfels Inclusions.*—Hornfels inclusions of very variable dimensions are the commonest type of xenolith, being found throughout the pluton. They are normally ovoid in shape and average 10–15 cms. along the greatest diameter. Near the contact exceptionally large masses over 100 feet in length occur, but elsewhere the maximum size does not generally exceed 20 cms. except in the case of the psammitic types. They are generally dark brown or black in colour due to the preponderance of biotite, and may present a schistose appearance in the hand specimen. Certain of the hornfels inclusions appear to have retained their original platy habit though they are vicarious as to distribution and orientation.

All the inclusions are characterized by the presence of abundant free quartz, occurring either as small angular grains or larger xenoblastic crystals. The quartz shows frequent development of irregular cracks and minute inclusions of the dust-liquid type are common.

The most abundant type of pelitic or semi-pelitic hornfels inclusion consists of biotite, cordierite, quartz and felspar, with these minerals occurring in various proportions.

Biotite is frequently the commonest constituent occurring as irregular flakes, or larger plates, which commonly include quartz, apatite, and magnetite. Pleochroism is marked with X = light yellow brown to Y and Z = dark reddish brown. Pleochroic haloes are abundant. The biotite generally shows a certain amount of alteration to chlorite or to muscovite. Rutilization may be developed parallel to the cleavage.

Cordierite occurs as poikiloblastic areas, or rounded or more rectangular crystals generally altered to dense sericitic aggregates, nests of muscovite and pinite often with fibrous or radiate structures. Alteration commences round the edges of the crystals and proceeds inwards along irregular cracks and cleavages. Most of the cordierite has suffered alteration, though there are occasional residuals of clear unaltered optically biaxial and negative cordierite. Inclusions are abundant, though with more complete recrystallization the cordierite is relatively free from inclusions and may show sector trilling. Pleochroic haloes are frequent about included zircons, being most pronounced where cordierite has been altered to secondary products.

Where biotite and cordierite are abundant, and form about 90 per cent. of the rock by volume, the inclusions contain andalusite and spinel included in the cores of cordierite crystals. The andalusite forms rounded anhedral crystals showing faint pleochroism in shades of pink.

Plagioclase felspar is present in varying amounts and where it is abundant the cordierite percentage decreases, this inverse relationship being due to the variability in composition of the original sediments. The composition is that of oligoclase (An_{28}). Albite twinning is practically universal, the twin

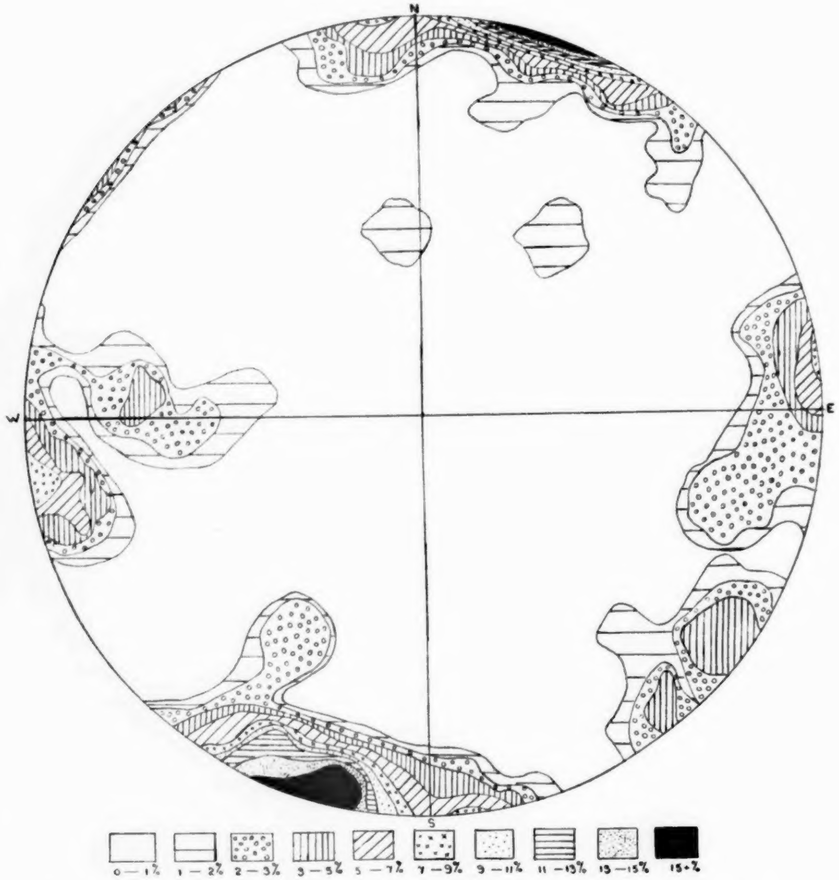


FIG. 6.—Stereographic projections of 100 joint directions mapped at Castle Rock area.

lamellae frequently being very fine. The greater proportion is more or less intensely altered to sericite.

Muscovite is a fairly prominent constituent but in the main is secondary after cordierite or biotite. Accessories include magnetite, apatite, sphene, and zircon. Spinel, probably of a variety of pleonaste, was only noted in one section as greenish-brown subhedral grains. Biotite, and to a lesser extent cordierite, are occasionally partially replaced by brown tourmaline.

In all these hornfels inclusions potash felspar is present, though in very variable amounts. It replaces plagioclase and quartz, showing slight alteration to dusty kaolinitic products. In contrast to the other constituents it does not form part of the phasal assemblage due to simple thermal recrystallization but has been introduced from the magma.

The mineralogical composition of typical hornfels inclusions is reflected in the micrometric data given in Table I. The modal compositions were determined with a Dollar integrating stage. The lengths of the traverses were over two hundred times greater than the longest continuous intercept made by any mineral in the sections measured. Potash felspar is conceivably slightly low but the probable error is not greater than 3 per cent.

Chemical analyses (Table II) indicate a high percentage of potash, a high alumina percentage (due to abundant cordierite), and high magnesia.

A cordierite-biotite hornfels with quartz and a variable percentage of felspar is typical of the hornfels inclusions found throughout the granite pluton. One xenolith from south of Hout Bay proved to be a cordierite-andalusite-biotite-hornfels containing quartz and plagioclase, with spinel as an armoured relic included in the cores of poikiloblastic cordierite crystals. The presence of spinel is ascribed to a deficiency of silica in those parts of the xenolith and freezing of the surrounding magma before the attainment of equilibrium. A similar type of inclusion was recorded from Camps Bay by Scholtz (1947, p. lvii), though it contains sillimanite in place of andalusite.

Psammitic hornfels xenoliths (Plate XXII, photo 2) are also common throughout the pluton. Megascopically they are generally lighter in colour than the pelitic or semi-pelitic hornfels types. Microscopically they are seen to consist essentially of quartz, felspar, and biotite. Quartz is the most abundant constituent, and with felspar is present in amounts in excess of those in the pelitic hornfelses (Table I). Biotite is less common and may show a rude parallelism. Accessories include cordierite, magnetite, apatite, sphene, and zircon. The constituent minerals do not differ in their optical properties from those described above.

Chemical analyses reflect a high silica and low alumina percentage (Table II). As in the pelitic and semi-pelitic inclusions there has been a marked fixation in potash.

TABLE I.—MICROMETRIC DATA.

Modes of Malmesbury Xenoliths in the Peninsula Granite.

	Normal Granite	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Quartz	31·3	31·5	31·70	24·0	25·1	37·4	42·9	32·0	30·6	38·8	30·1	34·8
Potash felspar	28·4	present	16·5	9·4	12·5	27·2	26·4	27·7	24·7	20·8	34·6	46·6
Plagioclase felspar	28·3	present		14·6	10·5	9·9	15·9	21·9	18·7	15·2	19·7	9·9
Biotite	9·4	30·9	29·2	28·2	26·7	21·5	13·3	12·2	22·5	24·7	14·8	7·2
Muscovite	2·5	present	present	0·8	present	0·9	1·5	3·2	present	present	0·2	1·4
Cordierite	—	37·5	22·6	22·9	25·1	3·1	present	2·5	—	0·1	—	—
Apatite	present	present	present	present	present	present	present	0·4	1·1	0·2	0·5	0·1
Iron ore	present	present	present	present	present	present	present	present	1·9	0·1	present	present
Sphene	—	—	—	—	—	—	present	present	0·4	present	present	present
Tourmaline	present	present	—	—	—	—	—	—	—	—	—	—
Total	99·9	99·90	100·0	99·9	99·9	100·0	100·0	99·9	99·9	99·9	99·9	100·0

Normal granite. Mathias, 1940, p. 198.

1. Cordierite biotite hornfels, Froggy Pond.
2. Cordierite biotite hornfels, Llandudno.
3. Cordierite biotite hornfels, Camps Bay.
4. Cordierite biotite hornfels, Bakouen.
5. Psammitic hornfels, Froggy Pond.
6. Psammitic hornfels, Millers Point.
7. Leucocratic cordierite bearing granitic xenolith, south of Bantry Bay.
8. Biotite rich microgranitic xenolith, Froggy Pond.
9. Biotite rich micrographic xenolith, Froggy Pond.
10. Biotite rich micrographic xenolith, North-eastern corner of Lui Bay.
11. Leucocratic granitic xenolith, Froggy Pond.

While mineralogically the hornfels inclusions do not show extreme variation they have a fairly extensive textural range though throughout they have a typical hornfels texture. In the case of the pelitic and semi-pelitic rock types the least recrystallized inclusions, represented by the large xenoliths close to the contact, are similar to the spotted hornfels of the contact aureole. Ovoid poikiloblastic areas of cordierite, averaging 1–3 mm. across, enclose numerous small unorientated flakes of biotite and small rounded crystals of quartz. The biotite of the groundmass shows fairly well-marked parallelism. More intense recrystallization causes the cordierite to form clearly defined poikiloblastic crystals containing inclusions of biotite, rounded crystals of quartz, iron oxides and occasionally andalusite and spinel. Finally, recrystallization results in the development of rounded porphyroblasts of cordierite lacking the abundant inclusions though occasional flakes of biotite and rounded crystals of quartz persist. Concomitantly the quartz and biotite increase in grain size, the biotite forming large flakes which frequently enclose quartz and lack the earlier parallelism. Completely recrystallized pelitic and semi-pelitic hornfels xenoliths assume a granoblastic texture, with porphyroblastic cordierite (grain size 0·5–2·5 mm.) and large plates of biotite in an interlocking mosaic of quartz (average grain size 1·5 mm.) and felspar (Plate XXIV, photo 2).

The psammitic hornfels xenoliths have also undergone recrystallization with the development of an equigranular or granoblastic texture. The grain size, which averages 0·5–1 mm., is commonly finer than that of the more pelitic hornfels xenoliths.

(b) *Granitic Inclusions.*—Certain of the xenoliths have undergone more profound reaction with the magma, and in the more advanced stages of incorporation they have been tranformed into "biotite-rich microgranitic material or medium grained leucocratic cordierite bearing granitoid rocks" (Scholtz, 1947, p. lxxi). These xenoliths, which are of variable size, though generally larger than the hornfels inclusions, occur right throughout the pluton without any relation either to the contacts or to the concentration of hornfels inclusions. One of the largest of these granitic inclusions is exemplified by the 40 feet thick lenticular xenolithic mass at Clifton (Plate XXII, photo 3), which consists of alternating dark biotite-rich and light biotite-poor layers. The bands are somewhat wavy, but apart from this only slight deformation has occurred. A detailed description has been given by Walker and Mathias (1947, p. 508), who considered that "the original sediment must have been characterized by rapid alternations between argillaceous and arenaceous layers". They concluded that this xenolith represents the final product of granitization by the magma with the attainment of phasal equilibrium.

Other large granitic xenoliths show a more spherical or rounded outline

TABLE II.—CHEMICAL ANALYSES AND CALCULATED ANALYSES.

Chemical Analyses.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
SiO_2	70·36	70·32	69·22	73·56	74·98	75·26	66·82	65·02	59·24	59·26	57·77	67·18	67·03
TiO_2	0·38	0·46	0·69	0·22	1·05	0·96	0·63	0·69	1·22	0·49	2·05	0·75	0·63
Al_2O_3	14·68	14·93	14·90	14·38	10·63	10·94	14·74	16·17	18·32	20·75	15·14	14·64	16·66
Fe_2O_3	0·39	0·17	0·44	0·23	0·27	0·36	0·60	0·16	0·34	0·94	0·56	0·54	0·48
FeO	2·92	2·92	2·38	1·77	4·64	3·52	5·52	6·04	6·72	5·27	9·88	5·11	3·96
MnO	0·03	—	0·47	0·05	0·04	0·04	0·06	0·33	0·09	0·09	0·19	0·07	0·27
MgO	1·24	1·19	0·95	0·12	1·33	1·62	3·26	2·89	3·47	3·08	3·52	1·82	1·84
CaO	1·92	1·88	1·25	1·38	2·08	0·68	1·66	0·92	1·33	0·48	1·44	1·38	0·70
Na_2O	2·35	2·06	2·92	3·38	2·19	3·13	2·28	1·83	2·84	1·62	2·63	2·82	2·59
K_2O	4·64	5·04	5·73	4·02	2·06	2·77	2·85	3·69	3·66	4·44	4·64	4·06	5·13
P_2O_5	—	0·06	0·12	0·14	0·17	0·05	0·17	0·08	0·05	0·07	0·44	0·29	—
H_2O^+	0·74	0·56	0·90	0·78	0·41	0·40	1·44	1·48	2·59	3·06	1·23	0·92	0·49
H_2O^-	0·18	0·14	0·02	0·09	0·09	nil	0·05	nil	0·20	0·14	0·12	0·05	0·11
Total	99·83	99·73	99·99	100·12	99·94	99·73	100·08	99·30	100·07	99·69	99·61	99·63	99·89

1. Normal Granite, quarry at Lower Cableway Station. Mathias, 1940, p. 198.
2. Normal Granite, Marine Drive, Llandudno. Coetzee, 1941, p. 199.
3. Tourmaline Granite, Millers Point, Calculated B_2O_3. Scholtz, 1947, Analysis 28*b*.
4. Marginal porphyritic granite, Kloof Quarry. Walker and Mathias, 1947, p. 517.
5. Psammitic hornfels, quarry on de Waal drive. Walker and Mathias, 1947, p. 517.
6. Psammitic hornfels, Kloof Quarry. Walker and Mathias, 1947, p. 517.
7. Semi-pelitic hornfels, slightly spotted, quarry on de Waal drive. Walker and Mathias, 1947, p. 517.
8. Spotted hornfels, old swimming pool, Sea Point. Walker and Mathias, 1947, p. 517.
9. Spotted hornfels, Kloof Quarry. Walker and Mathias, 1947, p. 517.
10. Biotite rich xenolith, Sea Point. Walker and Mathias, 1947, p. 517.
11. Micaceous band in xenolith, Lower Road, Clifton. Walker and Mathias, 1947, p. 517.
12. Light band in xenolith, Lower Road, Clifton. Walker and Mathias, 1947, p. 517.
13. Felspathized xenolith, Kloof Quarry. Spencer, 1938, p. 114.

Calculated Analyses.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
SiO_2 . . .	61·3	63·3	61·1	61·5	70·8	75·4	69·4	68·2	70·3	70·3	74·5
TiO_2 . . .	1·0	1·0	1·0	0·9	0·9	0·5	0·5	0·8	0·8	0·5	0·1
Al_2O_3 . . .	19·4	17·8	19·1	19·0	13·1	11·7	15·4	14·4	12·8	14·5	12·7
Fe_2O_3 . . .	1·4	1·2	1·1	1·2	0·9	0·6	0·7	1·0	1·1	0·6	0·4
FeO . . .	8·3	7·4	7·2	7·1	4·9	3·0	3·5	5·2	5·5	3·3	1·9
MgO . . .	5·3	4·1	4·1	4·2	1·7	0·9	1·4	1·5	1·7	1·0	0·6
CaO . . .	trace	1·0	0·9	0·6	0·6	1·0	1·4	1·1	0·9	1·2	0·6
Na_2O . . .	trace	1·3	1·2	1·1	1·2	1·8	2·4	1·9	1·6	2·2	1·7
K_2O . . .	3·3	2·9	4·3	4·4	5·9	5·1	5·5	5·9	5·3	6·4	7·5
Total . . .	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0

1. Cordierite biotite hornfels, Froggy Pond.
2. Cordierite biotite hornfels, Llandudno.
3. Cordierite biotite hornfels, Camps Bay.
4. Cordierite biotite hornfels, Bakouen.
5. Psammitic hornfels, Froggy Pond.
6. Psammitic hornfels, Millers Point.
7. Granitic xenolith, south of Bantry Bay.
8. Granitic xenolith, Froggy Pond.
9. Granitic xenolith, Froggy Pond.
10. Granitic xenolith, Lui Bay.
11. Granitic xenolith, Froggy Pond.

Numbers of calculated analyses correspond with modal numbers (Table I).

and may attain a diameter of up to 50 feet (Plate XXIII, photo 1). Banding is not conspicuous, though the larger granitic inclusions may themselves include biotite-rich schlieren or small rounded clots of cordierite-biotite hornfels.

The granitic xenoliths range in composition from biotite-rich to biotite-poor types but consist essentially of quartz, oligoclase, potash felspar and biotite with essentially the same optical properties as in the hornfels inclusions.

Biotite generally shows more intense alteration than in the hornfels inclusions. Alteration is mainly to chlorite with the occasional formation of fan-shaped radiating aggregates, while rutilization parallel to the cleavage is common. Alteration of the biotite is accompanied by the excretion of iron oxides and the formation of sphene. Biotite is commonly moulded on quartz grains, and rounded inclusions of quartz are frequent. The biotite plates may show irregular or frayed ends.

Oligoclase has the composition An_{26-30}. Alteration is to sericite and, where intense, discrete flakes of white mica causing a "spangled" effect may be present. Plagioclase crystals commonly have embayed margins and include rounded crystals of quartz as well as biotite, sphene, and apatite. As in the hornfels inclusions there has been a marked fixation of potash. Potash felspar replaces quartz and plagioclase felspar, and myrmekitic intergrowths are often developed at the boundaries with oligoclase. Potash felspar is present in variable amounts. It frequently forms large plates (up to 6 mm. in length), penetrating the other minerals irregularly and enclosing rounded and corroded quartz and plagioclase grains. Quartz inclusions range from large embayed plates to small optically continuous crystals or blebs, while the included plagioclase forms small, rounded subhedra or embayed and often skeletal plates. Carlsbad twinning is shown by a few individuals. The greater proportion is perthitic, with a minor amount of microcline microperthite.

Muscovitization has affected much of the potash felspar, its form and relationships suggesting a deuteric origin. Muscovite is in the main secondary.

Cordierite is ubiquitous though present in accessory amounts. It occurs as rounded or more rectangular crystals, averaging 2 mm. in length, often moulded round the ends of the biotite plates. Apatite is present throughout, frequently in large prisms which may attain a diameter of 1 mm. Magnetite, probably slightly titaniferous, occurs frequently as inclusions in biotite and is commonly surrounded by narrow shells of sphene. Sphene also occurs outside the biotite as anhedral or more prismatic grains. Fluorite is an uncommon accessory and it appears to be associated with the alteration of biotite to titaniferous minerals. Zircons, included in biotite and cordierite,

are surrounded by intense pleochroic haloes. Van der Lingen and Walker (1925, p. 76) have recorded the presence of xenotime in the Clifton xenolith, the xenotime occurring in all probability as inclusions in biotite.

Tourmaline forming stout crystals, pleochroic from light greenish brown to dark greenish brown, is occasionally present as a late stage replacement product of biotite and potash felspar (Plate XXIV, photo 3).

Micrometric data and chemical analyses are given in Tables I and II.

Compared with the modal composition for the normal granite, the granitic xenoliths are richer in biotite, though generally poorer in plagioclase felspar. Chemical analyses show a high percentage of potash though fixation of potash has evidently been differential; for xenoliths both richer and poorer in potash felspar than the normal granite are found.

The granitic inclusions are finer in grain size than the normal granite and frequently have a granitoid rather than a granoblastic texture. The texture of the biotite-rich microgranitic xenoliths is equigranular, with the average grain size of the quartz crystals being 0·75–1 mm. Plagioclase felspar grains are somewhat larger, averaging 1·5–2 mm. A type of porphyritic texture is occasionally developed with porphyroblasts of quartz (averaging 2 mm.) and olioclase (up to 4 mm.) in an equigranular base of quartz, oligoclase, potash felspar, and biotite. Xenoliths of this type evidently represent an intermediate stage in the development of the medium-grained leucocratic granitic xenoliths. The latter inclusions have a granitoid texture with quartz grains averaging 3 mm. The grain size of the plagioclase averages 2 mm. Potash felspar shows a very variable grain size ranging from 0·75 mm. in the biotite-rich microgranitic xenoliths to 6 mm. in the coarser leucocratic granitic inclusions. Isolated phenocrysts of alkali felspar comparable in size to those developed in the normal granite are occasionally present in the larger granitic xenoliths.

In the majority of the microgranitic xenoliths the cordierite percentage does not rise above accessory amounts and these xenoliths are considered to have been derived from the more psammitic Malmesbury sediments. Certain of these micrograniticrocks, however, contain from 10 to 15 per cent. of cordierite and probably represent a transitional stage during granitization of the pelitic hornfels xenoliths.

VI. Geochemical Changes.

Recent work by D. L. Reynolds (1946) has demonstrated that the sequence of geochemical changes leading to granitization, in rocks of all types, involve changes in two distinct stages. During the first stage of alteration there is an initial enrichment in cafemic constituents and/or

alkalis followed by a granite-forming process during which the rock is granitized (*i.e.* its composition approaches that of associated granite).

During the first stage of alteration the pelitic and semi-pelitic rock types, under the metasomatizing influence of granite magma, become molecularly desilicated relative to the molecular proportions of the bases present, due either to an increase in the total alkalis (felspathization) or to an increase in any or all of the cafemic constituents (basification) or to a combination of both processes. During the second stage silica and alkali are added, the composition of the "desilicated" rock being altered so as to approach that of the associated granite. Desilication dependent on basification is characterized by the increase and geochemical culmination of one or more of the minor constituents TiO_2, P_2O_5, and MnO.

The two stages outlined for pelitic and semi-pelitic sediments are not as easily distinguished in the alteration of psammitic rock types, as granitization in the latter instance is essentially a desilication process. The early stage appears to involve an enrichment in alkalis which is sometimes accompanied by geochemical culmination of one or more of the cafemic constituents and one or more of the minor constituents.

The sediments of the Malmesbury Series included in the Peninsula granite show evidence of these two processes and are considered to add further support to Reynolds' contention.

In the area under consideration the sediments show rapid alternations of composition causing a major difficulty as regards the investigation of the geochemical changes suffered by the Malmesbury xenoliths in the granite. This variability of composition makes it practically impossible to establish chemical identity between xenoliths and specific sediments of the Malmesbury Series. Twelve analyses given by Walker and Mathias (1947, p. 517), both of country rocks and inclusions, and eleven analyses of inclusions calculated from the modal data, have been utilized to plot the composition fields for the different rock types. It is felt that the nature of the chemical changes can be determined with reasonable accuracy by the comparison of those composition fields.

The analyses have been plotted on the modified von Wolff diagram (Poldervaart, 1949, p. 183) and the fields for the following rock types are shown. (Fig. 7*a*): (1) granite, (2) pelitic or semi-pelitic hornfels sediments, (3) pelitic or semi-pelitic hornfels inclusions, (4) psammitic hornfels sediments, (5) psammitic hornfels inclusions, (6) granitic inclusions. The field for pelitic and semi-pelitic inclusions lies farther away from the granite field than that for similar sediments, its position indicating that compared with the least altered sediments the inclusions, as a whole, are desilicated. Similarly, in the case of the psammitic rocks, the inclusions are desilicated with respect to the sediments. In both cases desilication is mainly dependent

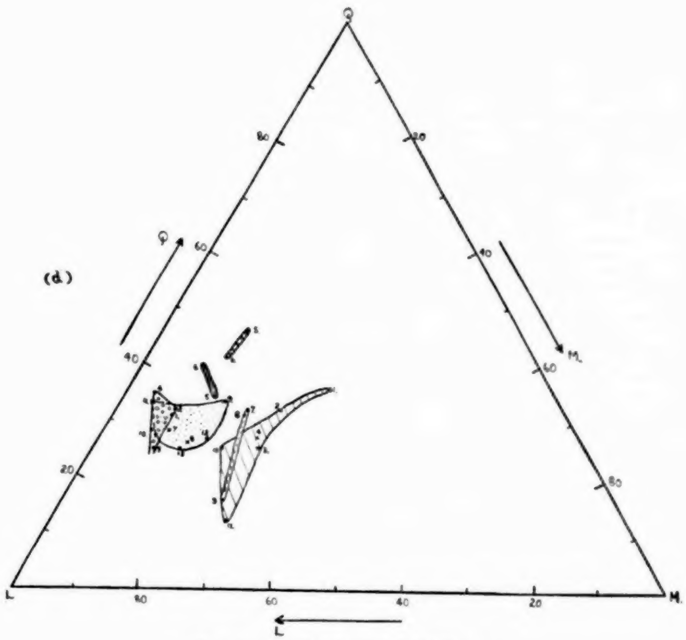
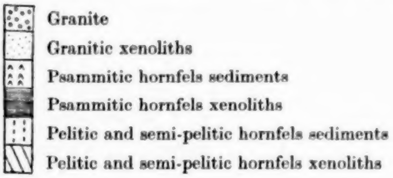
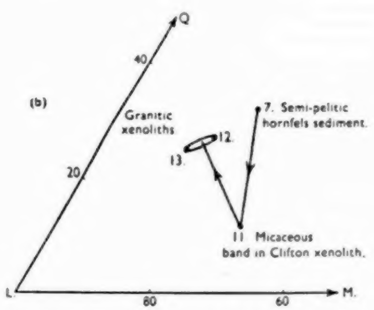


FIG. 7.—Modified von Wolff diagram.

Granite, sediments and xenoliths of the Peninsula area plotted on a von Wolff diagram. L = felspars. M = saturated melanocratics. Q = quartz. Dot = chemical analysis with number (Table II). Cross = calculated analysis with number (Table II).





Desilication with subsequent (or complementary) granitization of micaceous band in Clifton xenolith. Numbers refer to chemical analyses (Table II).

on felspathization. Granitic inclusions show a close approximation to the granite field.

Analysis 7 (Table II) represents the least altered type of semi-pelitic hornfels typical of the subordinate slaty intercalations in the neighbourhood of the granite. A comparison of this with the spotted hornfels from the contact zone (Analysis 9) shows that the contact hornfels is desilicated with respect to the unaltered type, the desilication being dependent mainly on basification with minor felspathization. There is an increase in alkali, alumina, and cafemic constituents while the summary of the geochemical changes (Table III) shows a geochemical culmination in the accessory constituents TiO_2 and MnO. The inclusions of pelitic and semi-pelitic types are in the main slightly silicated with respect to the contact sediments. Compared with the semi-pelitic hornfels from de Waal drive, however, they show geochemical culmination of alumina, FeO, and slight increase in alkalis.

The light band in the Clifton xenolith (Analysis 12) represents a completely granitized Malmesbury inclusions in phasal equilibrium with the magma. Comparison of this analysis (and the general field for granitic inclusions) with that of the biotite-rich xenolith (Analysis 10) show that during the second stage of alteration silica and alkali are added to the desilicated inclusions.

The psammitic hornfels at the contact (Analysis 6) is slightly enriched in alkalis and alumina as compared with the hornfels from De Waal drive quarry which has probably escaped appreciable alteration (Analysis 5). The change of composition, however, is slight and is possibly within the bounds of original chemical variation. Psammitic hornfels inclusions are definitely desilicated as compared with the corresponding sediments, the desilication being dependent mainly on felspathization. Granitization of the psammitic rock types appears to be merely an intensification of this desilication process, with an enrichment in alkalis, while FeO and the minor constituents P_2O_5 and MnO show geochemical culmination.

The chemical changes involved in the desilication of the Malmesbury sediments and the further chemical changes which took place during granitization of the desilicated products are summarized in Table III.

Reference has been made to the remarkable lenticular xenolith at Clifton showing alternating dark biotite-rich and light biotite-poor bands. The light bands have a coarse equigranular texture and are thoroughly granitic in the hand specimen, while the micaceous layers "have the megascopic appearance of a mafic mica syenite" (Walker and Mathias, 1947, p. 508). The chemical analyses reflect these characteristics (Analyses 11 and 12, Table II), and the light band represents the final product of granitization of Malmesbury sediments. The biotite-rich bands are poor in alumina as

compared with the biotite-rich xenoliths (Analysis 10) but are rich in K_2O, FeO, MnO, TiO_2, and P_2O_5, all of which Reynolds (1946) considers as constituents driven out by the fixation of Si, Ca, and Na. This suggests that the material driven from the light bands during granitization has been fixed in the micaceous layers; indicating either that desilication is followed by granitization or that the two processes are complementary. In either event the dark bands in this xenolith are considered to represent the most highly desilicated pelitic or semi-pelitic inclusions. Following this desilication there is a further stage of granitization. The relationships are shown on fig. 7*b* and Table III.

VII. Discussion.

Chemical changes leading to granitization of the Malmesbury sediments included in the granite involve in the case of the pelitic and semi-pelitic rock types a slight initial introduction of Al_2O_3, and one or more of the cafemic constituents and minor constituents. This was followed by an addition of alkalis and a small amount of silica, whilst alumina, cafemics and minor constituents tend to decrease. Psammitic inclusions show alkali enrichment accompanied by geochemical culmination of one or more of the cafemic constituents and minor constituents. A feature common to both arenaceous and argillaceous sedimentary inclusions is the marked fixation of potash, which is present in considerably greater amounts than in the hornfelses of the contact aureole. Mineralogically this is reflected in the xenoliths by the invariable replacement of plagioclase and quartz by potash felspar.

Walker and Mathias (1947, p. 515) found that the evidence for the basification of the Malmesbury sediments by an MgFe front, in advance of the alkaline emanations, was conflicting. The geochemical evidence indicates that there has been slight introduction of cafemics into the hornfelses near the contact. Chemical analyses and the composition of the contact sediments, however, lead to the conclusion that in the main the changes brought about in the Malmesbury hornfelses in the neighbourhood of the granite, and the initial alteration suffered by the inclusions, are largely the result of thermal metamorphism.

Early reconstruction of the shales and slates of the Malmesbury Series gave rise to cordierite or, where kaolin was abundant, to andalusite; while the quartz, felspar, and the biotite of the groundmass were recrystallized. At an early stage the cordierite formed poikiloblastic areas containing abundant inclusions which at a later stage became converted to biotite and quartz. In the further course of metamorphism, andalusite was converted to cordierite. The abundance of cordierite and the rarity of andalusite is to be expected because of the high magnesia content of the original sediments.

Table III.—Summary of Geochemical Changes.

A. *The Gains and Losses of Pelitic and Semi-Pelitic Rocks resulting in Desilication.*

	SiO_2	Al_2O_3	FeO	MgO	CaO	Na_2O	K_2O	H_2O^+	TiO_2	P_2O_5	MnO
Semi-pelitic hornfels (7) ⟶ Average spotted hornfels (8, 9).	$\ominus$	$\oplus$	$\oplus$	$\bigcirc$	–	$\bigcirc$	+	$\oplus$	$\oplus$	$\ominus$	$\oplus$
Semi-pelitic hornfels (7) ⟶ Biotite rich xenolith (10) .	$\ominus$	$\oplus$	$\oplus$	–	$\ominus$	$\ominus$	$\oplus$	$\oplus$	–	–	$\ominus$
Spotted hornfels (8) ⟶ Biotite rich xenolith (10) .	$\ominus$	$\oplus$	$\bigcirc$	$\oplus$	$\ominus$	$\ominus$	+	$\oplus$	–	$\bigcirc$	–
Semi-pelitic hornfels (8) ⟶ Micaceous band in the Clifton xenolith (11).	$\ominus$	$\oplus$	$\oplus$	$\oplus$	$\ominus$	$\oplus$	+	–	$\oplus$	$\oplus$	$\oplus$

B. *The Gains and Losses of Pelitic and Semi-Pelitic Rocks resulting in Granitization.*

	SiO_2	Al_2O_3	FeO	MgO	CaO	Na_2O	K_2O	H_2O^+	TiO_2	P_2O_5	MnO
Biotite rich xenolith (10) ⟶ Light band in the Clifton xenolith (12).	+	$\ominus$	–	–	+	$\oplus$	$\bigcirc$	–	$\oplus$	$\oplus$	–
Biotite rich xenolith (10) ⟶ Felspathized xenolith (13).	+	–	–	–	+	+	$\oplus$	$\ominus$	$\oplus$	n.d.	$\oplus$
Micaceous band in the Clifton xenolith (11) ⟶ Felspathized xenolith (13).	+	$\oplus$	–	–	$\ominus$	$\bigcirc$	$\oplus$	–	–	n.d.	$\oplus$
Micaceous band in the Clifton xenolith (11) ⟶ Light band in the Clifton xenolith (12).	+	$\ominus$	–	–	+	+	–	–	–	–	–

C. *The Gains and Losses of Psammitic Rocks resulting in Felspathization.*

	SiO_2	Al_2O_3	FeO	MgO	CaO	Na_2O	K_2O	H_2O^+	TiO_2	P_2O_5	MnO
Psammitic hornfels (5) ⟶ Psammitic hornfels (6)	⊕	+	–	⊕	⊖	⊕	+	–	–	⊖	○
Psammitic hornfels (5) ⟶ Average calculated hornfels inclusion.	–	+	–	○	⊖	⊖	⊕	n.d.	–	n.d.	n.d.
Psammitic hornfels (5) ⟶ Light band in the Clifton xenolith (12).	⊖	+	⊕	⊕	⊖	⊕	+	⊕	–	⊕	⊕

Arrows indicate change from the rock on the left to the rock on the right.

⊕ Denotes geochemical culmination.

⊖ Denotes geochemical depression.

○ Denotes no significant change.

Numbers in brackets refer to chemical analyses (Table II).

The early changes undergone by the xenoliths are strictly comparable to those of the contact hornfelses though there has been an intensification of this process. At the commencement of assimilation of the inclusions of Malmesbury sediments, thermal metamorphism altered the structure of the rock and there was a slight metasomatic introduction of cafemic constituents and alumina. The inclusions lost their crystalloblastic structure as the minerals became recrystallized. Quartz recrystallized freely. Early crystalloblastic patches of plagioclase, from the recrystallization of the detrital felspar, are small and have ill-defined borders. At a more advanced stage crystal faces begin to develop but relict inclusions of groundmass quartz and, to a lesser extent, biotite are still preserved. With recrystallization, biotite shows a tendency to develop crystal faces, and elongation parallel to the base asserts itself at an early stage. The grains begin to attain continuity, mainly in their marginal portions. This results in well-defined crystals still containing relict grains of groundmass quartz in their central parts. Where the process has been arrested prior to the complete attainment of crystallographic form, the biotite plates have irregular or frayed ends.

Metasomatism proceeded with the introduction of potash, and, to a lesser extent, of soda and silica, the hornfels xenoliths being converted to rocks of granitic composition. The potash was introduced either with or without alumina to form the alkali felspar which replaces the original plagioclase and quartz. Continued reaction results in the formation of more microcline and in the recrystallization of the other minerals. At a late stage there was a certain amount of muscovitization and tourmalinization. The completely granitized sediments, although in equilibrium with the granite in that the properties of their minerals correspond, contain more biotite and occasionally more potash felspar than the granite.

The various degrees of alteration of the cordierite have resulted from the metasomatic introduction of variable amounts of potash-rich alkaline material from the magma. The final product of alteration appears to be muscovite with pinite, representing an incomplete stage. The cordierite was originally formed largely from the sericite, chlorite, and to a small extent from the iron of the sediments. Under the influence of the potash-rich alkaline solutions this process is reversed.

Assuming that there is no real decrease in the amount of biotite present, it appears from the apparent decrease in the percentage of biotite that the bulk of the xenoliths has been increased slightly in volume during the formation of the granitic inclusions from the hornfels type.

Since the textures and relations indicate that fusion of the sediments did not occur, all of the processes of alteration are considered to have taken place in the solid rock by the diffusion of aqueous liquids carrying the

oxides. The solutions causing the granitising effects, from which potash was precipitated, must have had an excess of alkali over alumina and contained more potash than soda. The slight basicity of the plagioclase felspar of the xenoliths (An_{28}) as compared with the sodic oligoclase (An_{12}) of the sediments suggests that there may have been a certain introduction of lime. The solution may have contained a large or smaller amount of silica, though little silica is necessary to transform the sediments into rocks of granitic composition. The amount of material added, excepting potash, was probably not large, as the normal argillite, apart from a slight deficiency in alkalis and alumina, is not far from a granite in chemical composition. Spencer (1938, p. 114) considered that a xenolith from Kloof quarry (Analysis 13) would, if completely recrystallized, have been very similar to a normal granite.

The amount of alteration of these inclusions—the evidence of flakes apparently spalled off the main inclusion and transformed into schlieric aggregates or ghost xenoliths of biotite-rich granitic material—and the frequently ragged edges of the psammitic hornfels inclusions which often fade into the surrounding granite, all point to the conclusion that there must have been a great number of xenoliths which were completely absorbed in the granite. Evidence of contamination is provided by the occasional presence of almandine garnet in the granite and by the tendency of the biotite and cordierite to occur in clots. Rectangular crystals of cordierite attain a very high concentration in certain parts of the granite, these areas representing 'ghost xenoliths' which have been completely ingested.

While both the granite and the Malmesbury hornfelses are characterized by much the same heavy mineral assemblage, the main distribution of xenotime in a marginal zone determined by the proximity of the Malmesbury Series and its abundance in those areas of the granite characterized by the presence of cordierite (van der Lingen and A. R. E. Walker, 1925) probably provide further evidence of contamination.

Absorption of such a quantity of sedimentary material would modify the composition and characteristics of the granite chiefly by introduction of magnesia, alumina, and iron. This is thought to have caused a great increase in the amount of biotite. Mechanical disintegration of xenoliths has added, in particular, xenocrystal biotite and cordierite to the solidifying magma.

Inclusions of hornfels xenoliths are often surrounded by coarse granitic or pegmatitic segregations which may contain wisps of biotite-rich material. Contamination of the magma precipitating a pegmatoid phase with large phenocrysts of microcline microperthite on the lines of Bowen's reaction series would produce these pegmatitic facies. That they are not invariably present is considered to be due to the fact that the water contained in the

sediments (particularly if abundant) would undoubtedly assist in the diffusion of the solutions causing this crystallization.

Walker and Mathias (1947, p. 509) concluded that "the intruded granite crystallized as a non-porphyritic biotite granite" and that the large crystals of perthitic microcline were formed by late potassic solution circulating "throughout the big felspar granite of the Cape Peninsula". While the question of the origin of the granite does not fall strictly within the limits of the present paper, it is felt that this theory of the mode of formation of these phenocrysts is open to criticism.

In a recent criticism, Spencer (1947) has demonstrated that these perthitic microclines could not have formed below a minimum temperature of 600 degrees Centigrade, which is "not far below the minimum temperature accepted for wet magmas but above those believed to have obtained during hydrothermal replacement (felspathization)". Walker and Mathias have stressed the embayed margins of the porphyritic microclines as indicative of late stage replacement phenomena, but it has been pointed out (Wells, 1947) that in micrograpites with a microcrystalline groundmass the phenocrysts, which were of early origin, showed embayed margins.

In the migmatite zone large felspar porphyroblasts are almost invariably bordered by rims of granitic material which trail off into the enveloping rock. This suggests that the felspars of the migmatites have crystallized from granitic material injected into the sedimentary layers during the mechanical mixing of granite and slate. Further, the included material in these porphyroblasts and the large felspars of the granite are essentially similar and not characteristic, in the former case, of the groundmass of the sedimentary portions of the migmatites which is exceedingly rich in cordierite and biotite, the latter often showing a rude parallelism.

The abundant xenoliths of the Malmesbury sediments included in the granite all exhibit a marked fixation of potash, but rarely show porphyroblasts of microcline. Where developed, there is generally evidence of penetration of the xenolith by granitic material.

An interesting specimen from near the contact at Kloof quarry has recently been described by Shand (1949, p. 1213). This specimen from the granite "shows a single, exceptionally large, inset composed of a core of microcline surrounded by a broad mantle of plagioclase". A full description of the crystal is given by Shand, who considers it to be of great significance, concluding that "the inset grew in a liquid environment".

The contact zone and the granite itself present many anomalous features, but it is concluded that the granite was intruded in an essentially mobile condition and that, at the time of formation of the contact phenomena now exposed, it was in an advanced state of crystallization. The solid phases, microcline, microperthite, and oligoclase, had commenced to separate.

Mechanical penetration and mixing of granite and slate aided by the residual alkaline and siliceous phase, in which the porphyritic crystals of alkali felspar were forming, give rise to the migmatite zone. The microcline phenocrysts are considered to be due to those causes which produce porphyritic granite—an extended period during which potash felspar alone was being precipitated in any quantity.

VIII. Summary.

The stereographic joint diagrams show marked uniformity with maxima striking WNW.-ESE. This direction parallels the direction of stretching of the Peninsula pluton, and on this basis the WNW.-ESE. trending joints have been classified as longitudinal joints. Cross directions strike NNE. and NNW. Prominent aplite dykes follow these directions.

The Malmesbury xenoliths in the granite fall into two major groups—hornfels xenoliths and granitic xenoliths. The latter represent completely granitized sediments. The xenoliths are of variable size, and local concentrations of small xenoliths are fairly frequent. Both types of xenolith are found throughout the pluton and there is no mineralogical variation or change in composition of inclusions found on different exposures. The degree of alteration does not bear any apparent relation to the proximity of the present contact.

The hornfels xenoliths show marked similarity to the sediments of the contact aureole but have been further recrystallized. Pelitic and semi-pelitic types have been slightly enriched in alumina and cafemic constituents under the metasomatizing influence of the granite. This enrichment has caused basification of the argillaceous sedimentary inclusions.

This was followed by granitization and conversion to the granitic type of xenolith, effected chiefly by the introduction of potash and other alkalis and silica.

Granitization of psammitic hornfels xenoliths has been due mainly to an increase in alkalis.

Granitic xenoliths comprise biotite-rich microgranitic material containing variable amounts of cordierite, and medium-grained leucocratic rocks. The former group are an intermediate stage in the granitization of the hornfels inclusions, those rich in cordierite being derived from the more highly argillaceous sediments.

All xenoliths exhibit a marked fixation of potash.

The granite is considered to have risen up the heart of an anticlinal fold in the Malmesbury Series at a time when the compressive forces were decreasing. The lack of primary flow structures and the restricted nature of the migmatite zone and contact aureole are consonant with intrusion

at shallow depth. Alternatively, extensive erosion has now exposed the structureless core of the pluton.

Crystallization proceeded with the formation of large phenocrysts of microcline microperthite, and before final consolidation mechanical mixing of granite and slate gave rise to the migmatite zone. The intrusion of the magma was accompanied by stoping of rafts of Malmesbury sediments now represented by the xenoliths found on all exposures. The granite converted certain of these xenoliths into granitoid rocks while complete digestion of others has enriched the magma in biotite and cordierite.

Acknowledgments.

Thanks are due to Professor F. Walker, under whose guidance the present work was carried out, for his helpful advice and criticism; and to Mr. A. O. Fuller to whom I am indebted for the photographic plates. I wish also to express my gratitude to the University for the Staff Research Fund grant awarded to me to cover travelling expenses.

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EXPLANATION OF PLATES.

Photographs.

PLATE XXII.

Photo. 1. Sandblasting of granite showing grooving on inclined surface, Camps Bay.

Photo. 2. Typical angular psammitic hornfels xenolith, Bachelors Cove.

Photo. 3. Lenticular xenolithic mass at Clifton, showing banding of biotite-rich and biotite-poor layers on lower right and discontinuous aplite above.

PLATE XXIII.

Photo. 1. Large medium-grained granitic xenolith between Bantry Bay and Clifton.

Photo. 2. Contact of above xenolith with normal granite showing clots of cordierite hornfels inclusions.

Photomicrographs.

PLATE XXIV.

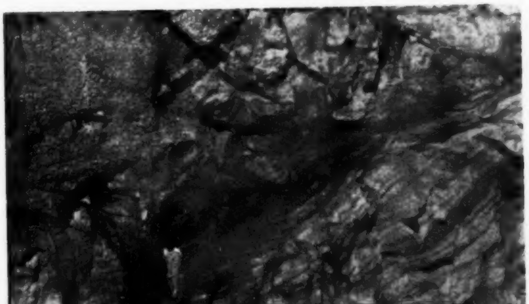
Photo. 1. Cordierite biotite hornfels, Llandudno. Poikiloblastic cordierite (lower right) encloses rounded crystals of quartz and small flakes of biotite. The biotite of the groundmass shows well-marked parallelism. Both biotite and quartz have been recrystallized. (Ordinary light.)

Photo. 2. Cordierite biotite hornfels, Froggy Pond. Porphyroblastic cordierite containing occasional inclusions of quartz and biotite and showing well-marked pleochroic haloes, and plates of biotite in an interlocking mosaic of quartz grains. (Ordinary light.)

Photo. 3. Leucocratic medium-grained inclusion, Millers Point. Stout crystals of tourmaline (centre) replacing biotite. The other constituent is quartz.

Photograph 1.

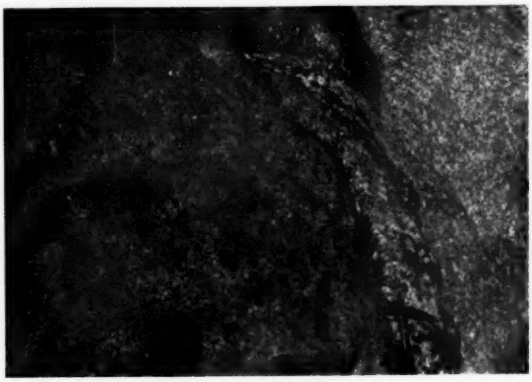
Photograph 2.



Photograph 3.

C. Boocock. Neill & Co. Ltd.

Photograph 1.



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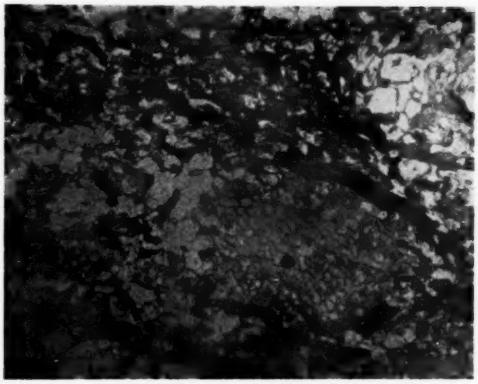

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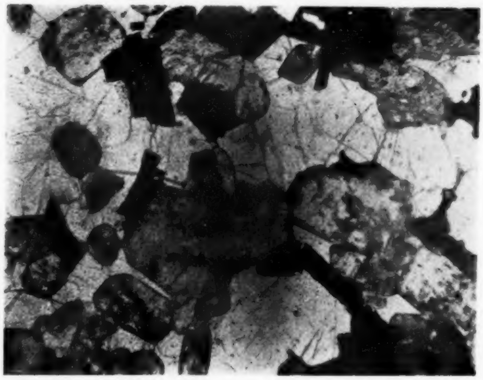

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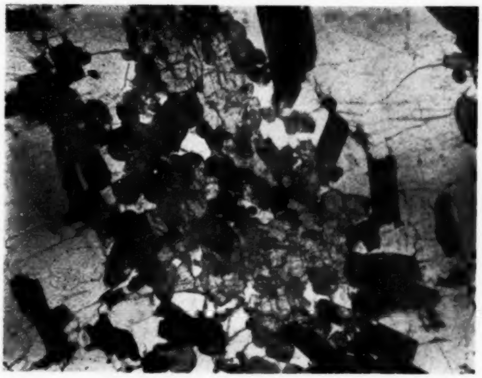

Photomicrograph 3.

C. Boocock. Neill & Co. Ltd.

DESCRIPTION OF A NEW SPECIES OF AMPHIPOD.

By K. H. Barnard, South African Museum.

(With three Text-figures.)

(Read August 16, 1950.)

Family AORIDAE.

Gen. Grandidierella Coutière.

1935. Barnard, Rec. Ind. Mus., vol. xxxvii, p. 295 (revision, key to species).
1936. Schellenberg, Zool. Anz., vol. cxvi, p. 154.

The investigation of South African estuaries by the University of Cape Town Ecological Survey has added three species of this genus to the fauna list. One is an Indian species whose presence in Zululand is not unexpected; another is a new species from the south-west Cape; the third has been described elsewhere.

The African species may be distinguished as follows:

1. 6th joint of gn. 1 ♂ broad . . . . *africana* Schell. (Cameroons).
2. 6th joint of gn. 1 ♂ narrow, at least basally.
   - *a.* Ventral spiniform process on segments 1 and 2 in (adult) ♂ . *bonnieri* Stebb.
   - *b.* No ventral processes.
     - i. Side-plates 1 and 2 with points. 2nd joint gn. 1 ♂ linear, 6th joint straight, without palm . . . . . *lignorum*.
     - ii. Side-plates 1 and 2 without points. 2nd joint gn. 1 ♂ widening distally, 6th joint curved, with transverse palm . . . . *lutosa* n.sp.
     - iii. Side-plates 1 and 2 very shallow, semicircular, without points. 2nd joint gn. 1 ♂ linear, 5th joint (adult), with strong basal spiniform process . . . . . *chelata* Brnrd.

Grandidierella bonnieri Stebb.

1935. Barnard, *l.c.*, p. 299, fig. 12, *d* (side-plates and ventral process), fig. 13, *b* (cross-section of 2nd joint of gn. 1 ♂).
1951. Id., Ann. Mag. Nat. Hist. (xii), iv., p. 708.

Port Canning, Bengal (Stebbing); Chilka Lake (Chilton); Cochin, Travancore, and Vizagapatam (Barnard).

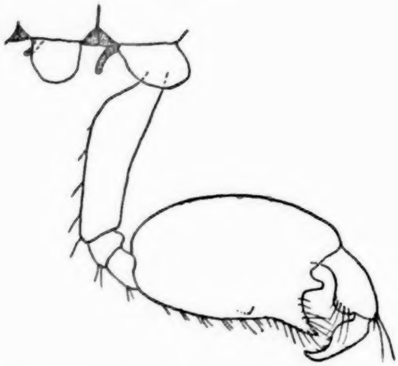

FIG. 1.—*Grandidierella bonnieri* Stebb. Gn. 1 ♂.

Richards Bay, and St. Lucia Bay, Zululand (U.C.T. Ecol. Survey, 1948 and 1949).

Grandidierella lignorum Brnrd.

1935. Barnard, *l.c.*, p. 300, fig. 14.

Keurbooms River estuary (Barnard).

Two specimens, which may possibly be this species, were found at Zoetendals Vlei, Bredasdorp Division, by Mr. A. C. Harrison, 1937.

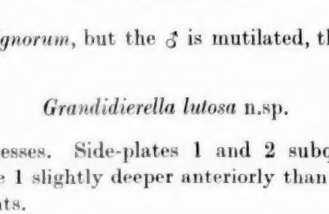

FIG. 2.—*Grandidierella lignorum* Brnrd. Gn. 1 ♂.

The ♀ agrees with *lignorum*, but the ♂ is mutilated, the gnathopods being missing.

Grandidierella lutosa n.sp.

No ventral processes. Side-plates 1 and 2 subquadrangular, longer than deep, side-plate 1 slightly deeper anteriorly than posteriorly, margins of both without points.

Antenna 2 ♂, flagellum 4(5)-jointed, with a stout spine on either side on each joint (as in *lignorum*); ♀ 3(4)-jointed, with slender spines.

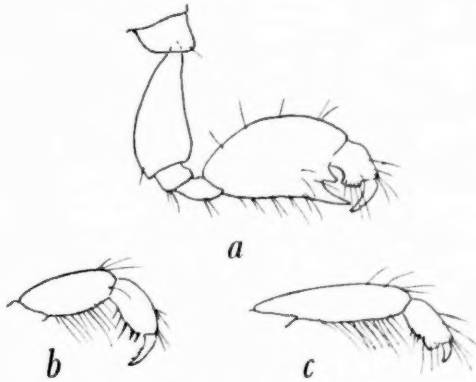

FIG. 3.—*Grandidierella lutosa* n. sp.
a. Gn. 1 ♂. *b*. Gn. 1 ♀. *c*. Gn. 2 ♂.

Gnathopod 1 ♂, 2nd joint flask-shaped, widening distally, cross-section ovoid; 5th joint ovoid, upper margin strongly convex, lower margin straight, ending in a strong pointed tooth, a smaller tooth between latter and junction of 6th joint; 6th joint stout, curved, outer and inner margins nearly parallel, palm transverse; 7th joint at base scarcely half the apical width of 6th, evenly curved. In ♀, 2nd joint not distally widened, 5th narrow ovoid, 6th shorter, with 2 spines on inner apex.

Gnathopod 2 ♂, 5th joint rather elongate, 6th parallel-sided, 2 spines on lower margin, palm transverse, 7th short. In ♀ similar but more slender, 5th joint not so elongate (6th subequal to its ventral margin).

Peraeopod 3, 5th and 6th joints with stout spines as in *lignorum*.

Peraeopods 4 and 5, 4th and 5th joints apparently without submarginal spines; hind margin of 2nd joint of prp. 4 with 3–4 setae, of prp. 5 with numerous plumose setae.

Uropod 3, ramus straight in both sexes.

Length: ♂ 5 mm., ovig. ♀ 3·5–4 mm. Greyish, with darker speckling, eyes black.

Klein River mouth, Hermanus, Cape Province. (U.C.T. Ecol. Survey, October 1948. ♂♂, ovig. ♀♀, in muddy sand.)

Grandidierella chelata Brnrd.

1951. Barnard, *l.c.*, p. 708, fig. 7 (gn. 1 ♂ adult and juv., gn. 1 ♀; gn. 2 ♂).
Estuaries of Port St. Johns, and Bashee River (U.C.T. Ecol. Survey, 1950).

My thanks are due to Professor J. H. Day and to Mr. Arthur Harrison for submitting for identification the very interesting collections of Amphipods and Isopods obtained during the course of the Survey, and for permitting me to describe this new species.

THE ECOLOGY OF SOUTH AFRICAN ESTUARIES.

Part II. The Klein River Estuary, Hermanus, Cape.

By K. M. F. Scott, Ph.D., A. D. Harrison, M.Sc., and W. Macnae, B.Sc.(Hons.),
Department of Zoology, University of Cape Town.

(With Plates XXV–XXVI and two Text-figures.)

(Read August 16, 1950.)

CONTENTS.

I. Introduction.

This paper embodies the results of a survey of the ecology of the fauna of the Klein River Estuary, situated about $3\frac{1}{2}$ miles from Hermanus, Western Cape Province, South Africa. The flora of the lagoon and its margins is dealt with incidentally.

This is the first survey of a South African estuary to be completed. The estuary is of particular interest as it is open to the sea at certain seasons of the year and closed by a sand-bar at others, whereas most European estuaries hitherto studied typically remain open to the sea throughout the year. While the Klein River estuary is open to the sea it is under a varying degree of marine influence. In addition to this, the state of the estuary is affected by the winter rains which both raise its level and lower its salinity. These two factors, rainfall and marine influence, interact in a somewhat complex manner according to the season, and the consequent salinity variations have a considerable effect on the fauna. As will be shown, the size of the mouth and its position in regard to the lagoon also have far-reaching effects on the main elements of the population.

The work was carried out by three members of the staff of the Department of Zoology, University of Cape Town, under the direction of Professor J. H. Day. It is hoped that the data obtained in this and similar surveys will be of considerable interest and value to the fishing and allied industries.

The field work of the survey was done during several visits in 1947, 1948 and 1949. Most of the investigations were carried out over periods of a few days at a time, supplemented by day visits when special circumstances demanded. Collections, observations and notes were made along both shores of the estuary and also from a boat.

II. Acknowledgments.

The authors wish to extend their grateful thanks to the specialists named below, who have so kindly identified much of the material collected during the survey, and without whose co-operation the results would have been valueless.

Flora: Professor R. S. Adamson (Cape Town); Dr. M. R. Levyns (Cape Town); Miss E. L. Stephens (Cape Town).
Polychaeta: Professor J. H. Day (Cape Town).
Crustacea: Dr. K. H. Barnard (South African Museum); Mrs. O. Tattersall; Dr. N. A. H. Millard (Cape Town).
Insecta: Dr. A. J. Hesse (South African Museum); Mrs. J. Omer-Cooper (Rhodes University College); Dr. J. Balfour-Browne (British Museum).
Mollusca: H. J. Koch; Dr. G. Ranson (Paris).
Fish: Professor J. L. B. Smith (Grahamstown).

We would also like to thank Mrs. M. M. Macnae, formerly of the Department of Botany, University of Cape Town, for assistance in the botanical side of the work, and Dr. G. J. Broekhuysen of the Zoology Department for criticising the section on birds. Messrs. Selkirk and Prillevitz of

Hermanus have given us information regarding the occurrence of fishes in the lagoon, as has Mr. F. Talbot of the Zoology Department. Mr. I. Williams of Hermanus has also given us assistance with boats, and has procured specimens of fish and other organisms for us, and we are much indebted to him.

We gratefully acknowledge financial aid from the South African Council for Scientific and Industrial Research, and from the University of Cape Town's Staff Research Fund.

Finally, we wish to thank Professor J. H. Day for his help and encouragement throughout the period of this research.

The Council desires to acknowledge the receipt of a grant from the University of Cape Town towards the cost of publication of this paper.

III. Methods.

The samples were collected by qualitative methods only, and no attempt has been made to obtain accurate quantitative samples.

The fauna of sand- and mud-banks above the water-line was dug out with a spade and washed in a coarse sieve of ¼ inch mesh. Smaller organisms were obtained by filtering and washing samples from the top inch or so of the sand and/or mud through grit gauze and coarse bolting cloth. Small stones and debris from the gravel beds were washed in hand nets of these materials. The addition of a small quantity of formalin to the washing water facilitates the collection of the organisms.

The fauna below the water-line was sampled with a D-net dredge and hand nets. The D-net was found to be most efficient in action and most of the samples were taken with it. The frame of this net is a semicircle of steel rod, with runners on the flat side to keep it on the surface of the sand or mud. The bag is of grit gauze protected on the under side by a coarser net. A dredge proved unsuitable, for it sank into the mud or soft sand almost as soon as it touched bottom and could not be dragged along.

A small purse seine (30 yards long, 3 feet high, and of ½ inch bar) was used with some success to catch small and juvenile fish in inlets near the mouth of the estuary.

Plankton samples were taken by day and by night with a fine plankton net.

Most of the samples were immediately preserved by the addition of formalin, and subsequently carefully sorted in the laboratory.

Water samples were taken in ½ pint beer bottles with spring caps and rubber rings, and the chlorinity titrated in the laboratory. In May and September 1947 the titrations were done under field conditions.

pH readings were taken on the spot, using a Lovibond comparator

and B.D.H. indicators, mainly Thymol Blue, and the readings modified in relation to salinity.

IV. Description of the Estuary.

The Klein River is a small but permanent stream which drains some 300 square miles of the Caledon District of the Western Cape Province (see map, fig. 1). Most of the area is an undulating grain-farming district

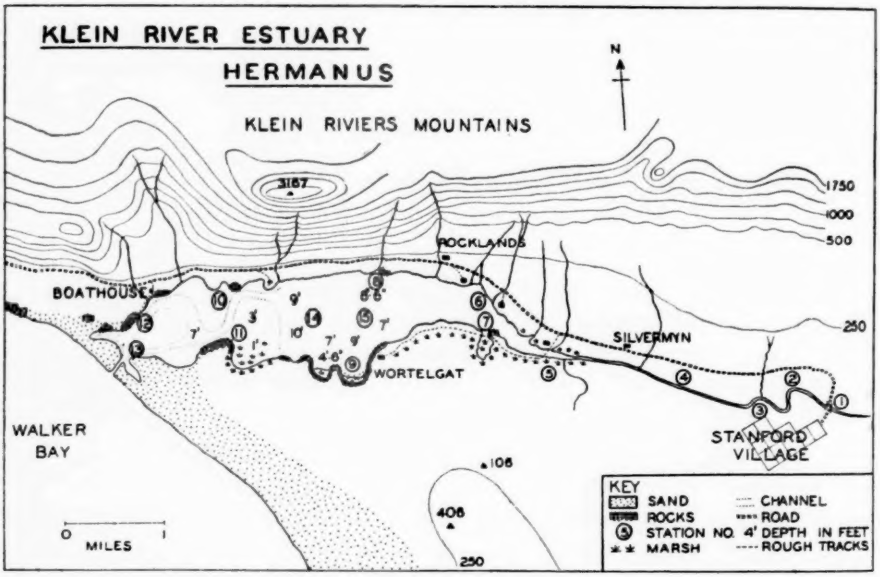

Fig. 1.

with a comparatively low rainfall (see Table I). The range of mountains lying to the north of the estuary has a fairly large rainfall but no rainfall station records it. As the river approaches the shores of Walker Bay on the southern coast of the Cape Province it runs from east to west, and as it approaches the sea broadens out into the lagoon and forms the estuary, which has a total length of 8 miles.

The estuary lies in the coastal plain along the base of the Klein Riviers Mountains, the highest peak of which is 3167 feet above sea-level. The mountains are composed of Table Mountain Sandstone, the undulating farmlands of Bokkeveld shales, and along the southern shore of the lagoon there are recent limestones overlaid by blown sand and clothed with thick bush.

TABLE I.—AVERAGE RAINFALL 1945–1949.

(From figures supplied by the Department of Transport's Weather Bureau.)

Rainfall Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Hermanus .	0·64	0·39	1·40	2·57	2·98	2·77	3·62	2·38	2·59	2·80	1·62	0·64	24·40
Stanford . .	0·44	0·18	1·71	2·02	3·25	2·24	3·12	2·54	2·09	3·39	1·23	1·07	23·28
Dunghyll Park.	0·15	0·10	1·05	1·02	1·49	1·65	1·83	1·29	1·08	1·66	0·67	0·34	12·51
Caledon . .	0·29	0·54	1·95	1·78	2·58	2·02	3·11	1·65	1·82	2·75	1·05	0·44	19·95

Most of the fresh water in the estuary comes from the river, which brings down rather muddy, slightly acid water (pH 6·9–7·0) when in flood, and clear, very slightly peat-stained water at other times. A large amount of clear peat-stained acid water (pH 5·0) also enters from the streams which rush down the Klein Riviers Mountains and flow into the north side of the lagoon and estuary. There is also some seepage of water from the limestone along the south shore of the lagoon.

The relative amount of water flowing into the estuary can be correlated with the rainfall figures. Lying in the winter rainfall area of the Western Cape Province, with a mild Mediterranean climate, the estuary and river basin are never subjected to extremes of temperature or flooding.

Over the district most of the rain falls between April and October, but some rain falls thoughout the year. Figures are available for four localities in the area under consideration; of these, three lie within the catchment area, and the remaining one, Hermanus, gives some indication of the minimum quantity falling on the Klein Riviers Mountains (see Table I). Actually this rainfall station is some 3½ miles from the mountains and does not appear to receive as much rain as they do. It will be noticed that the figures for Dunghyll Park are lower than the others because this station is in a region of rain shadow. The flow in the mountain streams falls off very rapidly during dry spells and towards the end of the summer becomes practically negligible. The flow in the river steadily decreases throughout the dry season and also finally becomes negligible. Good rain rapidly restores flow.

Although observations were made throughout the estuary, it was convenient that certain places should be investigated in greater detail. Thirteen stations were chosen along the shore, and are mentioned in the following pages as Stations 1 to 13. Observations made off-shore were related to these stations, with the exception that certain physical and

chemical records in the widest portion of the lagoon are listed separately as Stations 14 and 15. A list of these stations follows, and their situations will be seen on the map (fig. 1).

Station 1: Stanford Bridge, the most easterly point on the survey.
Station 2: Three-quarter mile downstream, where the river changes from a brook to a sluggish canal-like stretch.
Station 3: Below Stanford Village—$1\frac{1}{4}$ miles down from the bridge—chosen because this was the highest point to which estuarine animals had penetrated.
Station 4: Half-way between Stanford and the lagoon—typical of the canal-like stretch.
Station 5: Ford at head of lagoon—at junction between the canal-like stretch and the lagoon.
Stations 6, 7, 8, 9: All in the wider, upper section of the lagoon.
Stations 10, 11: On the channel in the lower reaches of the lagoon.
Stations 12, 13: At the seaward end of the lagoon.
Station 14: In the centre of the lagoon midway between Stations 10 and 9.
Station 15: In the centre of the lagoon midway between Stations 8 and 9.

The area studied can be divided naturally into three main sections, to wit, the river, the slow-running canal-like stretch, and the lagoon. A short description of each follows (see map, fig. 2).

(*a*) **The River.**

Just above the village of Stanford and some 8 miles from the seaward end of the lagoon, a road-bridge crosses the river, at this point quite fresh and flowing sometimes swiftly and sometimes imperceptibly. The river here is not influenced by the sea, except under exceptional circumstances. It flows between the steep reed- and rush-covered banks, and the bottom is muddy with occasional outcrops of shaly rocks and sandstone. This road-bridge was the highest point of the survey (Station 1).

The exceptional circumstances previously referred to were those obtaining in March 1950 when the estuary was closed and the water-level was unusually high. As will be explained later, this led to saline water reaching this point.

(*b*) **The Canal-like Stretch.**

About $\frac{3}{4}$ mile downstream from this bridge the river quite suddenly widens and becomes sluggish and canal-like, with very steeply sloping banks and reed- and rush-covered margins. At this point (Station 2) in

seasons 1947–49 no estuarine animals were found and the fauna was similar to that at the bridge. At Station 3, just below the village of Stanford, about 1¼ miles from the bridge the first estuarine animals (small mussels and amphipods) were found. The remaining 3 miles or so of the canal-like stretch are very uniform, and Station 4 about half-way down this length is typical of it.

The bottom of the river throughout the whole stretch is of coarse quartzitic sand, overlaid in places by layers of soft mud and detritus. The depth varies between 12 and 18 feet and the width from 50 to 200 feet. As one passes down this stretch the marine influence becomes more apparent.

(*c*) **The Lagoon.**

Head of Lagoon.—About 4 miles below the bridge the canal-like river widens into a shallow lagoon some 4 miles long and up to ½ mile wide. At the head of the lagoon, our Station 5, a ford crosses to reach the farms on the south side of the lagoon. Here, grass-covered banks and salt marshes stretch down to the water-level of winter and early spring. Below this level when the water is high, 12 to 30 inches of water cover a wide flat of sand overlaid by a thin layer of greasy mud. In summer, when the water-level is low, only a narrow channel remains, not more than a few inches deep, and the wind removes the thin layer of mud, leaving a sandy waste.

Depth of Lagoon.—Most of the lagoon consists of muddy shallows through which a deeper channel meanders. The depth of the lagoon varies from a few inches in the shallows to 10 to 15 feet in the channel. In the middle reaches of the lagoon the depth over the mud-banks on either side of the channel averages 2 to 5 feet. The largest area of deep water is in this stretch. In the lower reaches the average depth over the mud-flats is about 1½ to 3 feet, though deeper holes are frequent. These depths apply to early summer conditions and are correspondingly greater in the rainy season, when the level of the lagoon may be up to 4 feet higher.

North Bank.—Along the north bank of the lagoon several mountain streams enter the lagoon. They form small deltaic marshes at their mouths, and at such places the boggy shores are clothed with a sward of flowering plants. These deltas are separated by promontories of broken sandstone and beaches of quartzitic sand and gravel. Station 6, about ¾ mile from the ford mentioned above, includes one of these small deltas and a beach of stone and gravel. Station 8, about 1 mile farther down, includes one of the small promontories backed by bush and trees, and alongside it a small bay with margins of coarse sand, gravel and mud, and floored with fine sandy mud. A small stream pushes its delta into this bay. A mile

farther down, at Station 10, the shore is rocky in places and the channel sweeps close inshore.

South Bank.—The southern bank of the lagoon, on which lie Stations 7, 9 and 11, differs from the other both in conformation and appearance. A recent limestone forms low and scattered outcrops towards the head and foot of the lagoon, and low cliffs in the middle reaches. Here and there are small sandy beaches. Where the cliffs have receded some way back from the water's edge there are small salt marshes. No important streams flow in on this side but there is considerable seepage of water from the banks.

Stations 7 and 9 are opposite Stations 6 and 8 respectively. Station 7 is on a low rocky point next to a salt marsh, and Station 9 is in a sandy bay. In late summer the water at Station 7 had receded some 50 yards, leaving sandy mud covered with dead weed. At Station 9, where the bottom slopes more steeply, the water did not recede so far, but a crust of dried weed had formed on the surface of the shallow water.

Station 11 is on a low limestone promontory $1\frac{1}{4}$ miles from the mouth, and the channel runs past it on the way from Station 10 to the sea. Between these stations the channel flows past two mud-flats covered with *Ruppia maritima*, which form a good hunting-ground for birds. The bottom on these flats is of soft muddy sand, and only in a few places is it firm enough for one to walk with ease.

Foot of Lagoon.—Towards the seaward end of the lagoon the bottom becomes firmer and more sandy. Near the mouth, the channel divides into two branches round a low tidal sand-bank, covered by the tide when the mouth is open and by flood-waters when the mouth is closed. The north channel is floored with hard sand with occasional muddy patches, and there are outcrops of sandstone along much of the shore. The seaward end of these rocks and their surroundings were chosen as Station 12. The south channel has very little mud, a hard sandy bottom and a few weed patches. Station 13 is on the south channel, in the sandy shallows where the mouth was cut in 1947 and 1948. These two channels have deeper holes, probably not more than 12 feet deep.

The Open Lagoon.—During the summer months the lagoon is landlocked and the level gradually falls, being lowest in autumn. It fills up considerably with the winter rains. When the water-level has become sufficiently high to threaten the neighbouring farm lands, a passage is dug through the sand-bar which separates the lagoon from the sea. This opening was made in July in 1947, and in September in 1948 and 1949. Forestry Department labourers dig a trench in the sand and allow a trickle to develop and pass over the beach to the sea. The water in the lagoon at this time is considerably higher than the sea. The trickle gradually enlarges and the

water finally breaks through with considerable force. The rush is sometimes dangerous to boats on the lagoon, and in September 1948 a boat and its occupants were washed out to sea, unable to row against the current. On this occasion the water was seen to drop very rapidly—over two feet in three hours. A considerable scouring of the channel in the lower reaches must accompany this rapid outflow of flood-water.

The mouth remains open throughout the spring, and at this time the lagoon is fully tidal. The tidal range is not very great; in September 1947 it was about 12 inches at the foot, and in September 1948 about 30 inches. Both these observations were made near the mouth at neap-tides; no observations were made at spring-tides. When the mouth was beginning to close and the passage for water in and out was restricted and shallow, observations taken irregularly by Mr. I. Williams indicated that there is a fortnightly rise and fall in the average level of the lagoon, this being highest at spring- and lowest at neap-tide.

At spring-tides a considerable volume of water enters from the sea, and all of this does not, apparently, have time to ebb through the narrow mouth before the next tide flows. Hence low levels do not occur with spring-tides; on the contrary, each successive tide raises the general level a little. At neap-tides the amount of water entering is less, and so the amount of water forced into the lagoon at springs can run out and so produce lower levels, reaching a minimum a day or so after the smallest neap-tide. A similar phenomenon has been recorded by Bassindale (1943) as occurring in the narrower reaches of the Severn estuary.

As the bar is built up, the twice-daily tidal period at the foot of the lagoon is reduced until only the highest of spring-tides crosses the bar, and eventually the bar becomes too high even for these, and then the estuary is closed. The formation of the bar is due primarily to long-shore currents, and the speed with which it is built up depends on the strength of the outflow from the estuary. Winds also play a part in building the bar after it has begun to show itself between tides.

The lagoon is under tidal influence for a period varying from a few weeks to several months. This period depends on several factors. In the season 1948–49 the lagoon was still open in January, and the channel at the edge of the breakers was waist-deep. By the end of February it had closed. As noted above, the lagoon emptied with considerable violence, and the tidal currents, when the level had been reduced, were strong. Also, after the opening there was heavy rain during October which again scoured out the mouth (5 to 8 inches of rain over most of the area). On this occasion it had been opened opposite a large sand-bank and there was little scouring at the opening, and also tidal influence was only slight during the period when the mouth was open.

In 1947 the tidal rise and fall was only noticed at the foot of the lagoon. In October 1948, during neap-tides about three weeks after the lagoon had been opened, the tidal influence could be noticed at Station 5 at the head of the lagoon, with a small but definite difference in level of about 3 to 4 inches. The tidal waters rushed past Station 10 at considerable speed up into the middle reaches of the lagoon where, although to some extent dissipated, the current was noticeable when boating in the channel opposite Station 6 near the head of the lagoon.

The position in the bar at which the artificial mouth is dug varies from year to year. In the winter of 1946 the mouth was dug very close to the Hermanus end, just below Station 12. In 1947 and 1948 the mouth was dug just below Station 13, which place would seem to be the more natural outlet. In 1949 the opening was made almost half-way between these two, opposite a large sand-bank. The position of opening seems to influence the fauna in a manner to be discussed below.

V. Physical and Chemical Conditions.

(a) *Salinity* (see Table II).

The salinity records, though incomplete, give a fair indication of the conditions to be found in the lagoon and estuary. They show, as one would expect, that there are considerable variations of salinity, some of which are seasonal and some tidal.

When the lagoon is open to the sea the estuary is tidal and a normal estuarine salinity gradient is developed. Reference to the figures for September 1947 and October 1948 (see Table II) shows this clearly.

In October 1948, for example, when the mouth was widely open, clear, blue sea-water (salinity $33{\cdot}0°/_{oo}$) entered it on a flowing tide and spread out at the foot of the lagoon, pushing back the brown estuarine waters and setting up a strong current in the main channel. At Station 10, where the channel enters the middle reaches of the lagoon, on this flowing tide a salinity of $30{\cdot}9°/_{oo}$ was recorded, but it is not known how far into the middle reaches this water extended. As has been mentioned above, one could perceive the tidal current while boating off Station 6, in the upper reaches, and also that there was a small tidal difference of 3 to 4 inches at the head of the lagoon (Station 5) although there was no noticeable difference in salinity ($1{\cdot}1°/_{oo}$ at high water and $1{\cdot}0°/_{oo}$ at low water).

At low tide the brownish waters of the estuary flowed out to sea and discoloured the waters in the vicinity of the mouth. The low-tide figures again showed the salinity gradient in the lower reaches of the lagoon, though it is less steep (see Table II).

The figures for September 1947 also show the gradient clearly, although

TABLE II.—SALINITY.

Date.	Lagoon open or closed.	1	2	3	4	5	6	7	8	15	9	14	10	11	12	13
—/5/47	closed	0·73	..	..	7·14	10·07	..	..	..	..	..	..	..	33·34	33·71	..
—/9/47	open	..	0·36	0·36	..	0·81	9·60	15·05	20·75	..	16·85	..	21·92	22·01	31·67	30·43
1/3/48	closed	..	..	..	..	19·72	..	26·49	..	..	22·56	..	..	..	..	..
31/3/48	closed	0·53	..	0·61	2·29	2·88	22·70	..	21·87	..	..	..	25·08	25·77	27·75	..
—/5/48	closed	1·61	..	0·67	2·63	15·93	22·86	..	..	23·17	..	23·44	23·40	23·69	24·56	24·58
21/8/48	closed	..	..	..	7·93	12·30	10·86	..	13·95	..	..	..	13·84	..	14·45	..
23/9/48	just opened	..	..	..	1·18	..	..	..	9·78	..	..	..	..	..	12·59	..
20 to 22/10/48	open	..	..	..	..	1·16 H 1·02 L	9·11	0·75	8·10 H	..	11·00 L	13·26 L	17·52 L 30·93 H	16·04 L	17·97 L	33·08 H
24/2/49	closed	..	..	..	..	..	..	..	33·51	..	..	..	37·14	38·33	38·49	38·65
16/3/49	closed	..	..	..	..	..	..	..	..	..	..	..	..	..	..	38·73
11/4/49	closed	..	..	..	..	..	..	..	..	..	..	..	39·54	39·99	39·04	38·58
23/11/49	open	..	..	0·46	0·70	1·40	20·91	..	..	..	..	..	..	..	..	20·95

H, taken approx. at high tide. L, taken approx. at low tide.

tidal influence on this occasion was not nearly so strong and did not affect the estuary so much. The mouth was not so widely open as in 1948. These figures probably represent more nearly the conditions when the lagoon has just become shut off from the sea.

After the mouth is closed a mass of water is trapped, and this water may be expected to retain its salinity gradient for a short time. A strong south-east wind, deflected by the mountains to blow more or less down the lagoon from an easterly direction, blows the surface water down the lagoon and causes some mixing. Thus the salinity tends to become less steep. Reference to the figures for 31/3/48 will show this. As the lagoon fills up after the winter rains the salinity becomes less, but the gradient still persists.

In November 1949 the lagoon closed at the beginning of the month. Soon afterwards the river and streams came down quite strongly and the lagoon rapidly filled up to a level approximately 3 feet above its previous one. This was due to an exceptionally high rainfall in November, over 3 inches at most stations. It will be noticed that the salinities on the 23rd of November in the upper reaches of the lagoon (Station 6) and at the foot of the lagoon (Station 13), not far from the place where the mouth had been cut, are more or less identical (20·9‰ and 21·0‰), apparently showing an almost complete lack of a salinity gradient in the closed lagoon.

Whether a gradient persists over the short period of a few days after the artificial opening, while the lagoon is emptying and before it has become tidal, is not-known. But this would not be of much importance.

So far as we have seen, and with this possible exception, there is no time when there is no salinity gradient in the estuary, even though it does tend to disappear at the end of the rainy season.

In the late summer and autumn of February and April 1949 the salinities at the foot of the lagoon were much higher than in previous years. At this time the salinity in the lower reaches was higher than normal sea-water (see Table II). The mouth had remained open much longer than usual, and was still open when the amount of fresh water entering was negligible. It may well be that, due to this, the mass of water enclosed was more saline than in previous years (contrast the figures for March 1948, in which season the mouth had closed early, and those for November 1949, when the mouth had again closed early, after which heavy rainfall had caused a large inflow of fresh water). Also, as was noticed in April, at high water of springs the sea comes across the bar, and runnels on the lagoonward slope of the bar indicate that there is some seepage of sea-water into the lagoon, even when the waves do not break over the top. In these circumstances, evaporation of water from the lagoon explains the high figures obtained.

In August 1948 the salinity at Station 4, in the middle of the canal-like

stretch, was much higher than would be expected in mid-winter when the river was running quite strongly. The following suggestion is a possible explanation of this and other seasonal differences in salinity in the lagoon and estuary.

When there is little inflow of fresh water and no tidal currents, there are very few water movements in the lagoon and estuary except those set up by wind. The prevailing winds blow from the north-west in winter and from the south-east in summer. The mountain range to the north of the lagoon deflects these winds, so that they blow up and down the lagoon in a more or less westerly or easterly direction. Thus a north-wester blows more saline water up the lagoon and causes a greater degree of mixing than would otherwise be expected. Moderately saline water would then be piled up to the upper reaches and flow into the canal-like stretch, especially if the general water-level is high and there is a deep-water connection between the lagoon and the canal. This may happen even when the river is flowing quite strongly, for the depth and width of the canal-like stretch are very much greater than the depth and width of the river, so that any strong flow in the river would soon be dissipated. A strong south-easter would have the opposite effect and would blow less saline water down the lagoon, as has already been mentioned. These suggestions seem to fit our findings, but could only be proved by a carefully chosen series of samples taken while such conditions are operating.

The main factor influencing the movement of saline waters from the lagoon up into the canal-like stretch is the general water-level in the estuary, for, when this is high, this zone is continuous with the lagoon; when, however, it is low, as for instance when the estuary is open to the sea, the two zones are practically disconnected. As the level is usually only high in the rainy season this is the time when the salt moves up, especially during intermittent dry spells when the flow in the river is weak.

The back flow of saline water could be seen easily during the exceptional circumstances obtaining during March 1950. The estuary had closed early during the summer of 1949–50 and there had been late rains (over 3 inches at three rainfall stations in November), which made the late summer level as high as the normal late winter level. The flow in the river had stopped almost entirely and, during a strong north-west wind, currents, which were seen to extend to all water-levels, were running upstream at Stanford Bridge, and saline water had already reached this point and possibly higher.

(b) *Hydrogen-Ion Concentration* (see Table III).

No attempt has been made to obtain a complete range of pH figures over the whole year, but the values obtained do indicate the general conditions.

The water in the river is neutral or very slightly acid, having a value of 6·9 at Stanford Bridge in May 1947 and 7·0 about ¼ mile downstream in September of the same year. In the canal-like stretch the pH is more variable. When the river is flowing strongly it is neutral (7·1 in September 1947 and 7·2 in November 1949); when the flow is less strong it is alkaline (7·6 in May 1947).

TABLE III.—pH.

Date.	1	2	3	4	5	6	7	8	9	10	11	12	13
—/5/47 . . .	6·9	..	..	7·6	8·2	..	..	..	..	..	8·5	..	..
—/9/47 . . .	..	7·0	7·1	..	7·2	8·2	8·7	8·7	8·3	8·5	8·5	8·7	8·5
—/5/48 . . .	..	..	..	..	8·3	8·3	..	8·4	8·5	8·3	..	8·3	..
23/11/49 . . .	..	..	7·2	7·2	7·3	8·4	..	..	..	..	..	..	..

The lagoon is alkaline (8·2–8·7) at all times, even at the end of the rainy season when the river and streams are flowing strongly.

The mountain streams entering along the north bank pour large quantities of distinctly acid water (pH 5·0) into the lagoon, but this is very rapidly neutralised, presumably by the buffering effect of the sea-water. A pH of 8·2 was recorded at Station 6—which is just at the mouth of one of these streams—at a time when the stream was flowing strongly.

Considerable amounts of alkaline salts must be leached out from the limestone along the southern shore in addition to that derived from the sea. All pH values recorded were corrected for salinity.

(c) *Temperature.*

Few temperature records are available. In open water, in March 1948, the temperature was 27° C., in March 1949 it was 25° C., and in May 1948 the temperatures ranged from 17·3° C. to 16·5° C. Observations on other landlocked bodies of water along the coastal strip of the Western Cape Province show that the annual range of temperatures in such waters does not extend much beyond 12° C. in winter to 28° C. in summer, except in shallow sheltered margins.

(d) *Oxygen.*

No determinations of oxygen content were made. It would seem that enough oxygen is available for the support of animal life as amphipods and isopods were dredged at all depths. Here and there, however, there

are small patches round the edge where conditions in the dry season appear to be anaerobic as hydrogen sulphide is given off, but these are not important to the estuary as a whole.

(e) *Suspended Matter.*

Sea-water entering the lagoon, while it is tidal, is clear, and one can distinguish small objects on the bottom at depths of from 6 to 8 feet. Estuarine waters running out at low tide are coloured brown by dissolved humus, and contain a small amount of suspended matter, and one cannot distinguish anything on the bottom. When the lagoon is closed the water is more transparent, especially in sheltered areas, but it has a brown tinge. Plants have been brought up from all depths where dredging has been done, but fields of *Zostera* and *Ruppia* only develop in the shallower parts, where the water is less than 3 feet deep on the average.

Flood-waters from the river are silt-laden, and also stained slightly brown by humus. Flood-waters from the mountain streams are clear, but coloured a deep brown by similar colloidal vegetable matter.

In the lagoon the silt settles very rapidly and suspended silt is of little importance. In the canal-like stretch the waters remain somewhat turbid throughout the year.

Measurements made with a Secchi disc on 23/11/49, when the river and streams were running strongly and the mouth had just closed, illustrate the rapid settlement of silt. In the upper reaches of the canal-like stretch the 6-inch disc disappeared at 4½ inches; in the middle of this stretch it disappeared at 6½ inches and at the foot it could be seen down to 18 inches. In the upper reaches of the lagoon, off Station 6, the measurement was 5 feet 6 inches, though the water here was stained very brown. At the blind mouth of the lagoon the disc could be seen on the bottom, at a depth of 8 to 10 feet, even though the water was deeply brown.

In the rainy season the waters of the lagoon become strongly coloured with dissolved humus; during the dry season the brown colour becomes lighter but never quite disappears.

VI. Flora.

The following account of the flora of the estuary is far from complete, and only those plants which appeared to be of importance in relation to the animal ecology are mentioned. Fresh material was identified for us by the members of the Department of Botany (acknowledged above) and was then discarded.

The flora of each section of the estuary is discussed separately, for the

differences between sections are quite distinct although there is some slight overlap.

(*a*) The River.

In the shallows and along the margins just below Stanford Bridge grow thick patches of the creeping sedge, *Scirpus prolifer.* In such places it gives shelter to many insect naiads and larvae. In summer and early autumn, when the flow is negligible, a Charophyte and a green alga grow in isolated pools.

On the banks are clumps of sedges, *Scirpus littoralis* and *Cyperus textilis*, and small stretches are lined with "palmiet", *Priorium palmita*, which extends into the water. Higher up the bank, often mixing with the surrounding bush, are patches of the tall bamboo-like *Phragmites communis* and bulrushes (*Typha* sp.).

(*b*) The Canal-like Stretch.

The banks of this stretch are quite steep, and in many places there are no shallow marginal strips. Where such marginal strips have not been formed, the ordinary bush and veld communities come down to the rim of the bank. Where they have been developed, they are occupied by tall growths of *Phragmites communis* and *Typha* sp. and, accompanying them in the upper reaches only, *Cyperus textilis.* These plants afford important shelter for the animals living in this stretch.

(*c*) The Lagoon.

(1) *Bottom Flora.*

The most abundant plant in the lagoon is *Ruppia maritima.* It forms large fields in the shallower water (under 2 feet, summer depth). The largest fields are in the middle reaches, and it is less abundant at the foot of the lagoon, below Station 11, but still occurs in small patches, and also at the head of the lagoon where the mud-flats dry out before the *Ruppia* can reach its full luxuriance.

On one of the mud-flats near Station 7, in the upper reaches of the lagoon, a large patch of the aquatic composite, *Cotula myriophylloides*, was found in October 1948, when the salinity was very low (0·75°/$_{oo}$). Miss E. L. Stephens tells us that this plant is commonly found in very slightly brackish water, usually in pools and vleis which dry up in the summer. These conditions apply to the place where we found it.

In the more saline waters of the lower reaches of the lagoon *Zostera capensis* becomes abundant, particularly from Station 8 downwards. It

has been noticed that *Zostera* colonises deeper water than *Ruppia*, and often forms a fringe between the latter and the deeper channels. Only occasional patches are found in the reaches above Station 8. Throughout the lagoon, but chiefly in the middle reaches, these two grass-like plants are heavily epiphytised by several filamentous algae: *Ectocarpus* sp., *Polysiphonia* sp., *Rhodochorton* sp., *Cladophora* sp. and *Rhizoclonium* sp.

No attached plants have been found in the channel, but the dredge brought up masses of drifting weed, including *Enteromorpha* sp., *Cladophora* sp., *Ruppia* and *Zostera*.

In May 1947 there was a narrow belt of *Porphyra capensis* just above the water-line on the rocks near the foot of the lagoon at Station 12. The mouth had been opened in winter 1946 adjacent to these rocks, which probably accounts for its presence there. It has since disappeared. *Porphyra* was present on the rocks at Station 11 in 1948 and 1949, these being the nearest rocks to the mouth during these seasons.

Entermorpha sp. is abundant in some of the pools at the foot of the lagoon, and *Ulva* sp. accompanies it on various poles in the lower reaches in the immediate vicinity of the mouth. The surface of the sand in quieter reaches is discoloured by large numbers of diatoms.

(2) *Shore Flora.*

Along the north shore the bush and the veld extend to the top of the gravelly and rocky beaches. Only where marshy deltas are formed by the mountain streams are swards of moisture-loving plants developed, and species of *Juncus* and *Cotula* dominate these.

Conditions on the southern shore are on the whole similar except that there are also large salt marshes, some of which are flooded when the lagoon is high. On the lower parts of these marshes, extending to the edge of the summer level and usually under water in the winter, a typical *Salicornia* association, dominated by *Arthrocnemum africanum* and *Salicornia Meyeriana*, develops. Higher up, these two are interspersed by the coarse grass, *Sporobolus virginicus*, and a few patches of the rush, *Juncus Kraussi*; the former extends further towards the water than the latter. *Triglochin striatum* is also common on the mud, and higher up *Arthrocnemum capense*, sea-lavender (*Limonium equisetalum*), sea-heath (*Frankenia hirsuta*), and a sedge (*Scirpus venustulus*) are common.

VII. Fauna.

The lower reaches of the river itself were studied in order to learn something of the community which contributed to the fauna of the upper

portions of the estuary. In the canal-like stretch the saline influence becomes important, even though the salinity is low (0·3–7·9°/$_{oo}$). In the upper lagoon there is a wide salinity range, 0·75°/$_{oo}$ and 37·14°/$_{oo}$ having been recorded in different parts of it at different times (see Table II). The ford where the canal-like stretch flows into the lagoon (Station 5) is dealt with separately, as its fauna is similar either to that of the lagoon or of the canal-like stretch according to the time of year. In the lower lagoon there is usually a high salinity (12·6–40°/$_{oo}$).

In the description which follows each of these sections is dealt with in succession. While dealing with each section, such vertical zonation as occurs is described, and each different type of community is dealt with separately where it is convenient to do so.

(*a*) The River.

The river at Stanford Bridge is usually above all influence of the sea, and at such times the fauna is entirely fluviatile. The constitution of this fauna varies very little throughout the year, though it is naturally more concentrated when the water is low. There is little or no vertical zonation. Crawling forms, such as the naiads of dragon-flies, tend to be restricted to the shelter of *Scirpus prolifer* growing in the shallows. Notonectids and Corixids and other swimming forms were found in the open waters of the pools.

The bulk of the fauna on all visits consisted of aquatic insects. In the marginal *Scirpus prolifer*, naiads of the dragon-fly *Helothemus* sp. or *Trithemus* sp. (probably both, as adults of *Helothemus dorsalis* and *Trithemus arteriosa* were caught nearby), naiads of the dragon-flies *Aeschna minuscula* and *Annax imperator*, and of the damsel flies *Ischnura senegalensis*, *Pseudagrion* sp. and *Elattonura* sp., were all common.

Two Corixids (*Micronecta piccanin* forma *pardina* and *Sigara contortuplicata*) and four Notonectids (*Anisops* sp., *Enithares sobria*, *Plea pullula* and *Plea piccanina*) have been found here and have shown slight seasonal variations in numbers, which seem to be insignificant.

Gyrinid beetles were common in backwaters, and a few Dytiscid and Hydrophilid beetles occurred among the marginal weed.

Simuliid larvae were common on the stones in running water, and a few snails (*Succinea* sp. and *Burnupia* sp.) were present among them.

Small copepods and ostracods were abundant in the shallow waters when the river was low, and a few specimens of the Cladoceran, *Simosa vetuloides*, have been collected here. On each visit a few specimens of the freshwater crab, *Potamonautes perlatus*, were seen.

About ¾ mile downstream from the bridge the river begins to widen

out into the canal-like stretch (Station 2), but no differences in fauna were found.

(*b*) The Canal-like Stretch.

For practically its whole length the canal-like stretch is under some saline influence (salinity 0·36–7·9‰), and this becomes more marked as one proceeds downstream. About 1¼ miles from the bridge at Station 3, just below the village of Stanford, the saline influence is first noticeable, and here, among a community of river animals similar to that described above, estuarine amphipods and isopods, and the small estuarine mussel *Modiola capensis*, make their appearance. As one proceeds downstream the river forms become less abundant and the brackish-water forms more plentiful.

Attention has already been drawn to the varying conditions of salinity in this stretch of the estuary, and with this variation of salinity there is a corresponding variation of the constitution of the fauna. When the salinity is low, the freshwater organisms, mainly insects, are more abundant, and disappear or become very noticeably reduced in numbers with an increase in salinity.

It will be remembered that the river in this stretch is quite deep (12 to 18 feet), and that there is a narrow fringe of reeds and rushes. This vegetation gives shelter to most of the types of animals found in this stretch. Planktonic organisms live in the open water, and several crawling types on the coarse quartzitic sand of the bottom.

Some of the freshwater insects, viz. *Ischnura senegalensis* and *Cloeon* sp., would appear to be permanent residents, for they have been found at Station 4, in the middle of the stretch, at all seasons, even when the salinity was quite high (7·9‰). They would then seem to withstand salinities at least as high as that mentioned, which is the highest recorded for this station.

Other types appear to be sporadic, since we have only found them on a few occasions. These include Culicine larvae (common at Station 4 in March and a few in September 1948), Nepid nymphs (March 1948), Dytiscid and Hydrophilid larvae (common in September 1948), caddis larvae of *Argyrobothrus* sp. (a few in September 1948), and a single naiad of *Aeschna minuscula* (September 1948). *Plea pullula* and *P. piccanina* (Notonectidae), *Sigara contortuplicata* and *Micronecta scutellaris* (Corixidae), are also sporadic, but in the case of the last three, one of the occasions was in August 1948 when the salinity was high, which is surprising.

Several other forms were present only when the river was flowing rapidly after rain. For instance, *Micronecta piccanin* f. *pardina*, *Anisops* sp., and naiads of the Libellulids, *Helothemus* sp. or *Trithemus* sp., were found at the end of March 1948 under such circumstances.

The estuarine forms do not show these variations, and the following types were found in this stretch on most visits, or on all of them. The sphaeromid, *Pseudosphaeroma barnardi*, was always common and occasionally very abundant. It was by far the commonest organism at Station 4, and may almost be considered to be the characteristic animal of this stretch. The amphipods, *Parorchestia rectipalma* and *Melita zeylanica*, were usually to be found. The little estuarine mussel *Modiola capensis* was always attached in some numbers to the rushes. Occasional specimens of the crab *Hymenosoma orbiculare* have been found as far upstream as Station 3, and its zöeae were an important constituent of the plankton throughout the stretch in November 1949.

The plankton on this occasion contained large numbers of the mysid, *Rhopalophthalmus egregius*, and crawling over the bottom were several small polychaete worms, the tanaid, *Leptochelia savignyi*, the isopod, *Cirolana africana*, and juveniles of the isopod, *Cyathura carinata*.

(*c*) The Ford at the Head of the Lagoon.

At this ford, where the canal-like stretch widens out into the lagoon (Station 5), conditions are very variable from season to season, and there is a wide range of salinity (0·81–19·72 $^\circ/_{\circ\circ}$). In addition there is the great change in level already mentioned (p. 289). When the water in the estuary is high, the ford, about ¼ mile wide and up to 3 feet deep, is part of the upper end of the lagoon. In summer, when the level drops, the bottom becomes exposed and mostly covered with dry blown sand, and the outflow from the canal-like stretch forms a mere trickle running between barren sand-banks.

It is rather surprising that at times when the water has been high and the salinity low we have found no aquatic insects here, while they have been found when the water was low, even though on some of these occasions the salinity was considerable. At the beginning of March 1948, when the salinity was 19·7 $^\circ/_{\circ\circ}$, the highest recorded at this point, naiads of a mayfly, *Cloeon* sp., and imagines of *Sigara meridionalis* (Corixidae), were both common. At the end of the month, after some rain, when the stream was running more rapidly and the salinity had fallen to 2·9 $^\circ/_{\circ\circ}$, the insect population had increased in variety. Naiads of *Cloeon* sp. and of *Ischnura senegalensis* were fairly common with a few *Sigara contortuplicata*. The *S. meridionalis* had disappeared. Two species of Hydrophilid and two of Dytiscid beetles were also fairly common at both these times.

The amphipods *Melita zeylanica* and *Parorchestia rectipalma* are usually to be found here. The small estuarine crab *Hymenosoma orbiculare* was found here on one occasion only, in May 1947; its zöeae were common in November 1949. *Modiola capensis* can always be found here.

An interesting point is the sudden virtual disappearance of the Sphaeromid, *Pseudosphaeroma barnardi*, of which a few specimens were found in September 1947 and at no other time; its place here and in the lagoon is taken by *Exosphaeroma hylecoetes*.

Several animals found only in the lagoon make their first appearance at the ford. On an islet of sandy mud, well out in the lagoon, many holes of the mud-prawn *Callianassa kraussi* were found. Isolated holes were seen at the ford in the narrow channel and, in spring, on the flat of sandy mud on either side of it. One typically marine crab, *Cyclograpsus punctatus*, had penetrated as far as this point in May 1947, but has not been seen there since. A small snail, *Assiminea* sp., characteristic of the middle reaches of the lagoon, was also found in large numbers on the water plants and stems of *Phragmites*.

The fauna at this ford is more variable than in any other portion of the estuary. When the water-level is high this region is physically and ecologically continuous with the lagoon, and at such times its fauna is similar to that of the lagoon. When the water-level is low one finds a fauna similar to that of the canal-like stretch, and this in spite of a much higher salinity on some occasions (see above). It would seem that some factor other than salinity inhibits the development of a typical freshwater community when the water-level is high, even though the salinity be lower, than at times when the river is low. What this factor is has not been determined.

(*d*) **The Lagoon.**

The lagoon, which constitutes the remainder of the estuary, shows a considerable fluctuation of seasonal conditions but, surprisingly, these are not to any great extent reflected in the fauna. Apart from animals which for at least part of their existence are dependent on the sea, the fauna at each of our stations has been very similar in numbers and constitution at all seasons of the year. So far as these "marine" organisms are concerned their distribution and number, both of individuals and variety of species, is largely dependent on the extent of the tidal influence while the lagoon is open to the sea.

The salinity increases as one passes down the lagoon, especially when the mouth is open, but there is an occasional anomaly. For example, in October 1948 the salinity at Station 7 (on the south bank 1 mile down from the ford (see map, fig. 2)) was much lower than was expected ($0{\cdot}75\,°/_{\circ\circ}$), and one naiad of *Ischnura senegalensis* was found here. Apart from this single instance no freshwater animal has been found farther down the lagoon than the ford at Station 5.

(1) *Shore Fauna.*

Along all the shores of the lagoon there is a high-water mark of decaying weed—chiefly *Zostera* and *Ruppia*, with some *Enteromorpha* in the lower

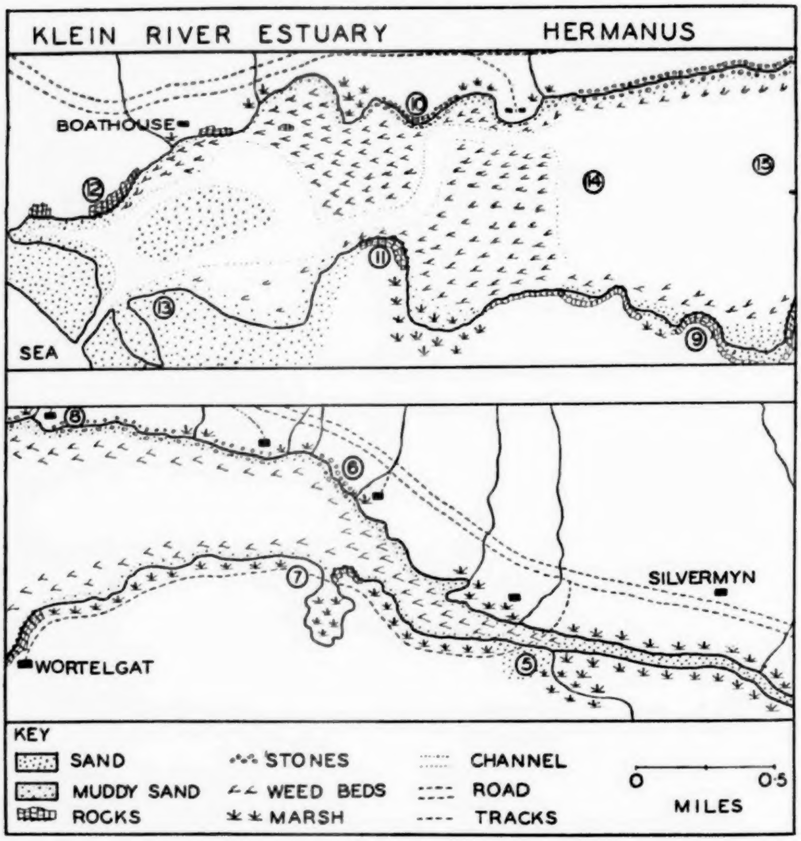

Fig. 2.

reaches. While this is still wet and comparatively fresh, it forms a mass of food for many animals, such as insects and their larvae, amphipods and isopods. The insects include several flies, beetles and Collembola, and also small crickets, *Tridactylus capensis*, in the sand on some beaches. Two common shore amphipods are abundant among the debris, *Talorchestia*

australis on the sandy beaches only, and *T. ancheidos* on gravelly beaches and under the weed on sandy beaches. The latter is found farther up the lagoon than the former, but neither reach the head of the lagoon. Among isopods are various land types, and of these *Porcellio* spp. are most numerous. Two littoral forms, *Ligia dilatata* and *Deto echinata*, are present in teeming masses where cover exists for them. Neither has been found at the ford at the head of the lagoon, but *Ligia* is abundant at Station 6 about 1 mile down on the north bank.

All these animals seem to prefer to be out of the water, although they may occasionally be found in the shallows close to the shore. There are others, which may sometimes be found in waterlogged sand and mud just above the water-line, but whose real habitat is in the off-shore shallows, and they will be discussed in that connection.

On outcrops of rocks, boulders and coarse gravel in the lower reaches a typically marine community establishes itself from time to time. All of them are typical intertidal shore forms, which seem to be hardy enough to withstand the lower salinity of the estuary. The periwinkles *Oxystele variegata* and *Littorina knysnaënsis* have been found upstream as far as Stations 8 and 10 in the middle reaches of the lagoon. At both these stations they were found on those rocks which were washed by the flood-tide. In 1947 both had persisted through the summer, and were quite common in May and even in September, indicating that they had survived the winter floods. They did not appear to survive the winter of 1948.

At Station 10 a greater variety of animals was found in January–April 1949, and included, in addition to the periwinkles already mentioned, young oysters (*Ostraea margaritacea*), young *Pyura stolonifera*, young *Mytilus* sp. (probably *M. perna*), small *Lima* sp. and *Chlamys* sp., small specimens of *Balanus trigonus*, *Marthasterias glacialis* and *Parechinus angulosus*. Apart from one young oyster of more than one inch across, all these animals had obviously settled while the estuary was open and the tide running past Station 10.

At the lower stations all these were also found with, in addition, *Oxystele tigrina*, *Siphonaria* sp., *Acanthochitona garnoti* and *Diodora* sp.

All these animals were found just on the water-line; also most of them were only found in May 1947 and in summer 1949. They did not seem to establish themselves in 1947–48 when the mouth was open for a comparatively short time only, and the tidal influence only slight. The flooding during the winter rains kills off all except the most hardy, and only the two, *Oxystele* spp., *Siphonaria* sp., and sometimes *Littorina knysnaënsis*, seem to persist over the winter.

The crab *Cyclograpsus punctatus* is common under stones on the shore, and has been found up to the head of the lagoon. As one would expect,

it is commoner along the north shore with its coarse gravel and boulders, than on the south shore where most of the beaches are sandy.

(2) *Fauna of Weed Beds.*

The weed beds of *Zostera* and *Ruppia* are very thickly populated with small animals. The amphipods, *Melita zeylanica* and *Corophium triaenonyx*, the isopod, *Exosphaeroma hylecoetes*, and the mysid, *Rhopalophthalmus egregius*, chironomid larvae, and a tiny snail, *Assiminea* sp., are often abundant. The distribution of any one of these is variable: it may occur in any patch of weed in large numbers or not at all, and each organism is fully independent of the others. No obvious factors influencing this variable distribution have so far come to light. These organisms seem to be more or less evenly distributed in all parts of the lagoon.

During the day the shrimp, *Leander pacificus*, is to be found among the weed, often in very large numbers. At night it may be found in any patch of open water and forms an important constituent of the night plankton.

Attached at the base of the weed and also among stones on gravelly bottoms, the small mussel, *Modiola capensis*, is also abundant and widespread throughout the length of the lagoon.

At the foot of the lagoon the crab, *Hymenosoma orbiculare*, and the molluscs, *Natica imperforata* and *Haminoea alfredensis*, are to be found crawling among the weed and also over the naked sand.

Among *Cotula myriophylloides* in the almost fresh water at Station 7 in October 1948, *Melita zeylanica* and *Corophium triaenonyx* were the only members of this assemblage present. It is also notable that on this occasion one naiad of *Ischnura senegalensis* was also found here.

(3) *Fauna of Bottom.*

The three main types of bottom found in the lagoon were investigated. These were mud, gravel and sand.

Mud Bottoms.—In the deeper parts of the lagoon, under some 6 to 8 feet or more of water, the bottom is not covered with weed and consists of a thinnish layer of mud on sand. Dredging on such a bottom with a coarse net brought up nothing, but the D-net samples indicated a rather sparse fauna of small crustacea. The commonest and most characteristic animals are the tanaid, *Leptochelia savignyi*, and a tiny isopod, *Paramunna* sp.; there were also small numbers of the isopod *Cyathura carinata*. In addition, small numbers of the mysid *Rhopalopthalmus egregius*, the isopod *Exosphaeroma hylecoetes*, and the amphipods *Corophium triaenonyx* and *Melita zeylanica*, were brought up. These may have wandered from the neighbouring weed-beds.

Gravel Bottoms.—Along the margin of the northern shore there are patches of gravel, or gravel and stone, in the shallows. This gravel is fairly clean, but often has a small amount of filamentous alga growing on it.

The most numerous and characteristic organism of this type of bottom is the talitrid *Parorchestia rectipalma*, but other organisms are also present; these include *Melita zeylanica*, *Corophium triaenonyx*, *Exosphaeroma hylecoetes*, numerous Capitellids and many small nematodes. It has also been observed that individuals of *Talorchestia ancheidos* frequently wander down from the gravel beach above. On one occasion (13/4/50) the tanaid *Tanais philetaerus* was common amongst the gravel off Station 6, but was not taken at other times.

Sand Bottoms.—At the lower end of the estuary, near the mouth, the bottom is mainly of sand with a small admixture of mud. The surface of this is covered with diatoms and Foraminifera (mainly of the family Miliolidae). Samples of the top one or two inches revealed a rich microfauna. The most characteristic animal is the amphipod *Grandidierella lutosa*, which is most abundant where the sand is firm and muddy. Other organisms which are numerous are small Spionids (*Prionospio* sp., near *malmgreni*), small Capitellids and minute nematodes. The bottom off Station 9 is of this type, though the Foraminifera are not present there, and diatoms are fewer in number. The fauna of the top two inches is similar to the above, except that no Spionids were found; also, in addition to the amphipod *Grandidierella lutosa*, *Corophium triaenonyx* was present, and there were a few *Parorchestia rectipalma*.

A similar bottom was investigated at Station 7, where the salinity was only $0{\cdot}75°/_{\circ\circ}$. Here the numbers of *G. lutosa* had fallen to insignificant proportions, and there were no *C. triaenonyx* or polychaets. *P. rectipalma* was still common. As the substratum was similar, it would seem that the drop in salinity had led to this change.

There are a number of larger animals found in, or associated with, sand bottoms in this estuary, but, as the following account will show, these are mostly confined to the foot of the lagoon.

Throughout the length of the lagoon the sand prawn, *Callianassa kraussi*, occurs frequently in very large numbers, both below the water-line and where the sand is waterlogged above it. In the upper reaches its numbers fall off fairly rapidly and it is not very common, though present at the ford at the head of the lagoon. Holes of *Solen capensis* are also abundant in the sandy shallows at the foot of the lagoon, and have been seen under water to a depth of about 4 feet. *Solen* tends to colonise firmer sand and is seldom to be found with *Callianassa*; this may be due to the fact that the branching galleries of the latter tend to make the sand unstable. The long slender polychaets, *Lumbriconereis fragilis* and *Nereis willeyi*,

were also dug from the waterlogged sand at the foot of the lagoon, and a few of the cone-shaped depressions characteristic of *Arenicola loveni* were noticed and the animals dug out.

Crawling over the sand in the shallows, and among floating weed, the small crab *Hymenosoma orbiculare* is numerous. It is most abundant in the lower reaches, but extends over the whole length of the estuary. At the foot of the lagoon the hermit-crab *Diogenes brevirostris*, and the Molluscs *Natica imperforata* and *Haminoea alfredensis*, are abundant in similar situations. Four Aplysiids, the large pale green *Bursatella leachi* var. *africana* and the three large brown or black and white species of Aplysia, are seasonally common, and crawl over the sand and among the weed in the shallows and in deeper water, but only in the lower reaches, as they have not been seen above Station 10.

In January–April 1949 large numbers of *Echinocardium cordatum* were found in the sand on either bank of the channel leading to the place where the lagoon had been open to the sea in the early summer. Judging by their numbers and size the colony had been established for some time, and later in 1949 evidence that they can withstand the winter flooding was forthcoming, for they were still abundant in the same place in September and October. They do not extend farther into the lagoon. In the same situation were also found several specimens of the marine crab *Ovalipes trimaculatus*, but these apparently did not survive the flooding.

In estuaries which are permanently open to the sea, it has been noticed that there may be a definite zone, where estuarine and marine water mix, which is inhabited predominantly by stenohaline marine animals, often in very large numbers. While such a condition does show signs of developing in the lower regions of this estuary when the mouth is open, this is only temporary and no such zone becomes well defined. However, there are certain animals which appear to be permanent inhabitants of the sand-bar at the mouth, which distinguish this area somewhat from the rest of the lagoon, so that it would appear to represent what may be an important zone in tidal estuaries. These animals include *Echinocardium cordatum*, *Arenicola loveni*, the mysid *Gastrosaccus gordonae*, the gastropod *Natica imperforata*, small burrowing lamellibranchs, *Tivela* sp., and possibly the crab *Ovalipes trimaculatus*.

VIII. List of Fauna with Biological Notes.

Phylum: **CNIDARIA.**
Class: **Hydrozoa.**
Order: **SIPHONOPHORA.**

Monophyidae (near *Muggiaea*). Station 13, incoming tide, 20/10/48.

Class: **Scyphozoa.**

Order: **RHIZOSTOMEAE.**

Medusae, fairly common all over lagoon in August 1948.

Phylum: **PLATYHELMINTHES.**

Class: **Turbellaria.**

Small turbellarians, common on stones at Station 6 and present in Canal Zone.

Phylum: **ASCHELMINTHES.**

Class: **Nematoda.**

Small nematodes in sand. Stations 9, 10, 12 and 13.

Phylum: **POLYZOA (ECTOPROCTA).**

Family: **Membraniporidae.**

Near *Membranipora (Electra) hastingsae* Marcus. Common, encrusting weed. Stations 6 to 12.

Phylum: **MOLLUSCA.**

Class: **Amphineura.**

Order: **LORICATA.**

Acanthochitona garnoti (Blainville). Rocks at Station 12, 1/5/47.

Class: **Lamellibranchiata.**

Order: **FILIBRANCHIATA.**

Mytilus sp. (juv.). Stones at Station 10, 11/4/49.

Modiola capensis Krauss.

This small mussel was common at all stations except Stations 1 and 2, where none was found. It was common under stones and attached to weed, and was also dredged from a depth of 10 feet in the channel, where it was rolled up in balls of mud and algae. (This may have been due to the action of the dredge or to the action of the current in the channel.) The specimens from the canal-like stretch were small and were attached, often in thick clusters, to the stems of *Phragmites*, etc.

Chlamys sp. Stones at Station 10, 11/4/49.

Order: **EULAMELLIBRANCHIATA.**

Ostrea magaritacea Lamark (*Ostrea iridescens* Gray of Professor T. A. Stephenson's Shore Survey).

During the visit in May 1947 several dead shells of this oyster were seen at Station 11, but no living specimens were found. In January 1949 young spat was seen at Station 10 and later at Station 11. In April the spat had grown sufficiently to be recognisable as belonging to this species.

Also on this occasion a single specimen of diameter 35 mm., which must have settled the previous year, was found.

Solen capensis Fischer.

The characteristic figure-of-eight holes of *S. capensis* were seen at several places at the foot of the lagoon, and specimens were extracted with a bent wire. *Solen* was not found farther up the lagoon than the large tidal sand-bank near the foot (see map, fig. 2). Below this it was common on the bottom in depths of four feet and less. Sand heavily colonised by the sand-prawn, *Callianassa kraussi*, was not favoured by *Solen*, probably because the activities of the prawn make the sand unstable and so unsuited to the type of hole *Solen* prefers.

Tivela sp. Sand at Station 13, 11/4/49.
Lima sp. Stones at Station 10, 11/4/49.
Donax serra. Sand at Station 12, 1/5/47.
Pisidium sp. River at Station 1, 1/3/48.

Class: **Gastropoda.**
Order: **STREPTONEURA.**
Tribe: DOCOGLOSSA.
Helcion pruinosa (Krauss). Rocks at Station 11, 11/4/49.
Tribe: RHIPIDOGLOSSA.
Diodora sp. Rocks at Station 12, 1/5/47.

Oxystele variegata (Anton).
Oxystele tigrina (Dillwyn).

These two species seem to behave in a similar way to *L. knysnaënsis* (see below). *O. variegata* has been found at the same stations on the same visits. *O. tigrina* was not found at Station 8 but was present at the other stations mentioned after the lagoon had been open for some time.

Tribe: TAENIOGLOSSA.

Littorina knysnaënsis Phil.

This species was found just above the water-line on rocks which were or had been directly washed by the tidal current at Stations 12, 11, 10 and 8 in May 1947, at Stations 12, 11 and 10 in September 1947, and at Stations 11, 10 and 8 in January to April 1949. No specimens were found in 1948.

Eggs or larvae would seem to enter with the tide and settle on available rocks, where they grow and develop until conditions become unsuitable. It was noticed that at Station 10 this small periwinkle occurred only on

rocks past which the tidal current flowed, while rocks, apparently similar, a short distance away, but not washed by the tidal current, were searched in vain for this animal.

Assiminea sp.

These small molluscs occur all over the lagoon from Station 12 to Station 5. They are sometimes found on the surface of clean sand or on stones, but they occur in their greatest numbers in weed beds. Here they may be extremely abundant, and sometimes constituted the main bulk of samples taken by D-net.

Natica imperforata Gray. Sand at Station 12.

Tribe: STENOGLOSSA.

Bullia sp. Sand at Station 13.

Order: **EUTHYNEURA.**

Tribe: TECTIBRANCHIATA.

Haminea alfredensis Bartsch.

This small Tectibranch is seasonally abundant at the lower stations in the lagoon. It occurs chiefly among weed, but may also be found crawling over the sand. Its yellowish egg ribbons are laid in autumn among the weed or attached to any solid objects under water.

Aplysia spp.

Large specimens (up to 12 inches long) of three species of *Aplysia* were common from January to March 1949, and were not seen on any other occasion. They were most common in the channel and in the shallows near Station 13, where the mouth had been opened earlier in the season, and became less common as one passed upstream, none being found above Station 10. Specimens of these three species were very much alike in colour pattern except for a few black and white variants of one of them. The three species were not distinguished in the field, and when they were subsequently separated in the laboratory it was too late to make field observations on them. Two of the three species seem to be new, at least in South Africa, and the third is *Aplysia capensis* O'Donoghue.

Bursatella leachii, de Blainville, var. *africana* Engel.

Large specimens (6 to 8 inches) of this Aplysiid were common each late summer and autumn. They were always most abundant in the channels in the immediate vicinity of the closed mouth, and in nearby backwaters.

Smaller specimens, about two inches long, were first seen in deeper water in December and January, and larger specimens, up to eight inches long, were found laying eggs in shallower water in May 1947 and April 1949. These large individuals were seen in deeper water up to the end of August 1947 and early September 1949, but no specimens were ever seen by us later in September or earlier than December. The long greenish egg strings were laid among the weed, in long tangles, chiefly in the shallows. It would appear that these Molluscs are detritus feeders or feed on the diatom scum on the surface of the sand, for the gut is always found to be full of sand.

Tribe: NUDIBRANCHIATA.

Dorids, rocks at Station 11, 24/2/49, and Station 10, 11/4/49.

Sub-order: **PULMONATA.**

Siphonaria aspera Krauss. Rocks at Station 12, 1/5/47 and 31/3/48.

Siphonaria capensis Q & G. Rocks at Station 12, 1/5/47.

Siphonaria oculus Krauss. Rocks at Station 12, 31/3/48.

Ancylus (*Burnupia*) sp. Station 1, common.

Succinea sp. Station 1, common.

Phylum: **ANNELIDA.**

Class: **Sipunculoidea.**

Small sipunculids, sand at Station 12, 28/5/48.

Class: **Polychaeta.**

Family: **Nereidae.**

Nereis willeyi Day. Sand at Station 12, and among tests of *Pyura* at Station 13.

Perinereis falsovariegata Monro. Among tests of *Pyura* at Station 12.

Nereis sp. (Juvs.). Station 4.

Platynereis dumerilii (Audouin and M. Edw.). In *Entermorpha* at Station 13.

Ceratonereis sp. Stations 4 and 5, bottom.

Family: **Eunicidae.**

Lumbriconereis fragilis (O. F. Müller). Sand at Station 12.

Lysidice capensis Grube. Amongst tests of *Pyura*. Station 12.

Family: **Nepthyidae.**

Nepthys sp. Sand at Station 12.

Family: **Aphroditidae.**

Lepidonotus clava (Mont.) var. *semitecta* (Stimps.). On Pyura at Station 13, 18/8/49.

Family: **Arenicolidae.**

Arenicola loveni Kinberg. Sand at Stations 12 and 13.

Family: **Spionidae.**

Prionospio sp. near *P. malmgreni* Claparède. From sand, mud and weed, Stations 4 to 13.

Family: **Capitellidae.**

Capitella capitata (Fabr.). From weed and sand, Stations 10 to 13.

Capitellids (genus and species unknown). Muddy sand. Station 9.

Family: **Sabellidae.**

Sabellids, ? *Oridia capensis* Monro. Stations 3 to 5.

Phylum: **ARTHROPODA**.

Sub-phylum: **CRUSTACEA.**

Class: **Branchiopoda.**

Order: **CLADOCERA.**

Simosa vetuloides (G. O. Sars). In river, Station 1.

Class: **Ostracoda.**

Small ostracods were very common in the river and in the Canal Zone, especially *Stenocypris* sp.

Class: **Copepoda.**

Cyclopoids and Harpacticoids were common in plankton all over the estuary.

Class: **Cirripedia.**

Chthamalus dentatus Krauss. Rocks at Station 12, 31/5/48.

Balanus trigonus Darwin. Rocks at Station 11, 24/2/49.

Balanus amphitrite Darwin var. *denticulata* Broch. Rocks at Station 12, 1/5/47.

Class: **Malacostraca.**

Divisions: PERACARIDA.

Order: **MYSIDACEA.**

Rhopalophthalmus egregius Hansen.

This mysid has been found, sometimes abundantly, throughout the length of the lagoon and in the canal-like stretch.

Gastrosaccus gordonae O. Tat.

This species has only been found at the very foot of the lagoon, on two occasions—in September 1948, while the lagoon was emptying just after the opening of the mouth, thus indicating that it had been in the lagoon during the winter, and later in October 1948, when it was caught on an incoming tide. It is apparently a marine form which can live under estuarine conditions.

Gastrosaccus brevifissura. Station 13, incoming tide, 20/10/48.

Mesopodopsis slabberi Van Beneden. Station 13, incoming tide, 20/10/48.

Leptomysis tattersalli O.S.T. Station 13, incoming tide; 20/10/48.

Order: **ISOPODA.**

Ligia dilatata Brdt. var. *gracilior* Brnrd.
Deto echinata Guérin.

It is convenient to deal with these two littoral species together, for their habits are very similar. Both occur abundantly in the lower and middle reaches of the lagoon, wherever adequate cover exists for them. They were found in teeming masses under large stones on rocky and gravelly beaches, and less commonly under weed cast up on the high-water mark. *Ligia* is by far the more abundant of the two. *Deto* does not wander so far from the water's edge, nor has it been found so far up the lagoon. Both were abundant at Stations 12, 11, 10 and 8 on all visits, but *Ligia* alone was found at Station 6. They have not been found farther up the estuary, chiefly because the type of cover they seem to prefer is lacking.

Paramunna sp. All over lagoon and Canal Zone, especially on muddy bottoms.

Corallana africana Brnrd. Canal Zone and Station 5.

Exosphaeroma hylecoetes Brnrd.

Decaying masses of weed in the lagoon provide a feeding-ground for large numbers of the estuarine Sphaeromid *E. hylecoetes*. The numbers of this animal in the catch seem to fluctuate with the amount of unattached and floating weed which is brought up with the D-net or dredge. It also crawls ashore to feed on decaying weed stranded there, but is then always found in wet places. It is also abundant under stones just at the water-line on the coarse gravel beaches on the north shore. It has been found at all stations from Station 4 downwards, but not above this. At Station 4 it was found on only one occasion. It is replaced in the canal-like stretch by the next species.

Pseudosphaeroma barnardi Monod.

This species inhabits similar situations to *E. hylecoetes* in the waters of medium and low salinity (less than $8°/_{oo}$) of the canal-like stretch of the estuary. *P. barnardi* has not been found in the body of the lagoon, and has been found at Station 5 on only one occasion. It has, however, been found in the mouths of several of the mountain streams running into the lagoon on its north shore. It does not extend far up the streams. Dr. K. H. Barnard has recorded this Sphaeromid from the mouth of a small stream running directly into the sea near the Old Harbour at Hermanus. Apparently it has a limited salt tolerance, and since it is not found far up

the streams it also dislikes completely fresh water, and tends to inhabit a sharply demarcated zone where fresh and brackish water meet.

Cyathura carinata (Kröyer). From Stations 4 to 13, few.

Order: **TANAIDACEA.**

Leptochelia savignyi (Kröyer).

This small tanaid is characteristically found in the top layer of mud, and has been collected throughout the estuary wherever the bottom is covered with a layer of mud.

Tanais philetaerus Stebb. In weeds and in algae, Stations 6, 9 and 11.

Order: **AMPHIPODA.**

Melita zeylanica Stebb.

This species has been found throughout the estuary except at Stations 1 and 2. It has not been found out of the water among stranded weed or under stones, but it was taken, often abundantly, among weed, whether this was growing or loose. In August and September 1948 none were found except for a few specimens at Station 11; it was, however, quite common in September 1947, some months after the lagoon had been opened to the sea. It may therefore show a minimum when the lagoon is full after the winter rains. In May it was really abundant, in some cases totalling 84 per cent. of the total D-net catch, and many juveniles were seen on this occasion, though breeding takes place in a smaller way throughout the year.

Paramoera capensis (Dana).

This species has been found living on weed and flotsam in and near the mouth of the lagoon. Specimens were only found while the mouth remained open. It would appear, then, that this species enters from the sea but is unable to establish itself in the lagoon.

Ceradocus aviceps Brnrd. One male at Station 3, September 1947.

Talorchestia australis Brnrd.

T. australis is abundant on all sandy beaches up to Station 9. Specimens may be found under decaying jetsam, both animal and vegetable, cast up on the high-water mark and even beyond it. They also make burrows in the sand, particularly underneath the jetsam. These burrows may be 2 to 2½ inches deep in soft sand. They have been taken at the foot

of the lagoon with D-net and dredge, as they swim about in water over sandy bottoms. A number of fingerlings of White Steenbras (*Lithognathus lithognathus*) caught in a small seine were found to have been feeding on this species almost to the exclusion of any other animal. *T. australis* was never found on rocky or gravelly shores.

This is the common sandhopper on sandy shores along Walker Bay.

Talorchestia ancheidos Brnrd.

T. ancheidos is also abundant, but it differs considerably in habit from *T. australis*. *T. ancheidos* is the commonest sandhopper to be found under stones on the gravelly beaches. Although it has been found among and under jetsam on sandy beaches it apparently does not burrow and, unlike *T. australis*, it has not so far been found on naked sand. It has been taken as far up the lagoon as Station 6, at all stations except Station 13; its apparent absence here may be due to the lack of cover.

Parorchestia rectipalma Brnrd.

This species has been found from Station 3 downward and is common. In the canal-like stretch it is found in the shelter of reed beds and in the lagoon, principally among stones on gravelly bottoms. It has been dredged with decaying vegetation and also found among freshly stranded weed.

None was found in May 1948. In August 1948 several females carrying eggs were found at Station 4, and this is the only record of breeding we have noted. At this time the level of the water was high, and the salinity in the canal-like stretch higher than usual.

Corophium triaenonyx Stebb.

C. triaenonyx is common at all stations except Stations 1 and 2. It lives in small tubes on the leaves and stems of water weeds and on the surface of stones or muddy sand.

Siphonoecetes sp. Station 13, incoming tide, 20/10/48.

Grandidierella lutosa Brnrd.

Abundant at all stations in the lagoon, this species lives in tiny burrows in the top inch of the muddy sand, and extends above low-water mark, provided the surface layers of the muddy sand are waterlogged. This is a new species, and a description of it by Dr. K. H. Barnard is included at the end of this paper.

Phronimid amphipod (Brachyscelidae). Station 13, incoming tide, 20/10/48.

Division: EUCARIDA.

Order: **EUPHAUSIACEA.**

Euphausid. Station 13, incoming tide, 20/10/48.

Order: **DECAPODA.**

Sub-order: **MACRURA.**

Leander pacificus Stimps. Fairly common in lagoon, especially in weed beds.

Sub-order: **BRACHYURA.**

Cyclograpsus punctatus M. Edw.

This marine crab is common under stones on the coarse gravel beaches of the north shore and much less common on the south shore, where it may sometimes be found in shallow burrows. It has been found as far up the lagoon as Station 5, and so seems capable of living in water of salinity as low as 9·6°/$_{oo}$.

Ovalipes trimaculatus (de Haan).

A typically marine crab, this species was first taken by the D-net near Station 13 while the lagoon was closed in May 1948. In April 1949 it was found to be quite common in the sand under water, buried with only the antennae and eyes exposed, at Station 13. It was only found along the south shore of the lagoon and up to 400 yards from the foot. Probably it enters with the tide when the lagoon is open, and it seems unlikely that many survive the winter floods. Many dead specimens were found.

Planes minutus (Linn.). One at Station 13, 5/1/49.

Hymenosoma orbiculare Desmarest.

This typically estuarine crab has been found at all stations in the lagoon and once at Station 3. It is very common on the sand at the foot of the lagoon and much less common in the upper reaches. At Station 5 it has only been found on one occasion (May 1947). Young crabs were dredged and D-netted in 6 to 10 feet, but no adults have been found at these depths.

Berried females were found in September 1947 lying partially buried in the sand under a thin felt of filamentous algae. Males were exposed and crawling on the surface of the sand among the weed. Zöeae formed an important constituent of the plankton, both in the canal-like stretch and in the lagoon, in November 1949, in salinities ranging from 0·70 to 20·90°/$_{oo}$.

Sub-order: **ANOMURA.**

Callianassa kraussi Stebb.

Throughout the length of the lagoon, wherever the bottom is composed of sand or muddy sand in which permanent burrows can be made, one can see the holes of *Callianassa*. They are uncommon in the channel near Station 13, where the sand is in almost constant motion with the tidal currents when the lagoon is open. In the backwaters towards Station 12 they become abundant, and in one particularly dense area 25 holes were counted in one square foot. In the sandy bay at Station 9 they are equally abundant, and are common on the sand near Station 7; a few holes are present at Station 5. On the north shore their holes can be seen on the sand in the bays under some 1 to 2 feet of water.

In completely calm water each hole is surrounded by a small cone of sand thrown out by the occupant. Each burrow has two openings, and perhaps more than two, some distance apart from one another. As it is difficult to dig out the animals, the number of holes will give some idea of their abundance, but does not represent an absolute figure. The burrows do not go straight downwards but twist about and cross and recross one another. As a result, the sand in areas with a high population is very unstable and one often sinks in up to the ankles.

Collections have not been made regularly, but females in berry have been found in October, and Stage 1 larvae were collected from a pool as the lagoon emptied on 2nd September 1949.

Diogenes brevirostris Stimps. Stations 12 and 13, on sand.

Class: **Insecta.**

Order: **ORTHOPTERA.**

Tridactylus capensis Sauss (Gryllidae). Common on sandy beach at Station 9.

Order: **EPHEMEROPTERA.**

Cloeon sp. Nymphs, Canal Zone and Station 5 in March 1948.

Order: **ODONATA.**

Sub-order: **ZYGOPTERA.**

Ischnura senegalensis (Rambur). Adults ♀ ♂, Station 1. Nymphs, Canal Zone and Stations 5 and 7.

Ellatoneura sp. Nymphs common at Station 1.

Pseudagrion sp. Nymphs common at Station 1. Present at Station 3.

Sub-order: **ANISOPTERA.**

Aeschna minuscula MacLach. Nymphs in river and Canal Zone. Few.

Orthetrum capense Calvert. Adult ♂ at Station 1.

Helothemus dorsalis (Rambur). Adult ♂ near Station 1.

Trithemus arteriosa (Burm.). Adult ♂ near Station 1. Nymphs of *Trithemus* or *Helothemus* were found at Stations 1 and 3.

Mesogomphus sp. Nymph, mouth of stream at Station 6, 25/9/47.

Order: **HEMIPTERA.**

Sub-order: **HETEROPTERA.**

Family: **Notonectidae.**

The following Notonectids have been found:—

Plea piccanina Hutch.
Plea pullula Stål.
Enithares sobria Stål.
Anisops sp. (nymphs only).

Only the species of *Plea* were found to extend into the canal-like stretch, and both were found here when the salinity was 7·9°/₀₀. The others occurred in fresh water only.

First instar nymphs of *Anisops* sp. and *Enithares* sp. (probably *E. sobria*, of which adults were found nearby) appeared at the end of March 1948, after heavy rain, but were not present at the beginning of the month. This may indicate that these species begin to breed during March, or that the onset of breeding may be affected by the first heavy rain.

Family: **Corixidae.**

Four representatives of this family have been found in the Klein River and its estuary. These are:

Sigara contortuplicata (Kirk.).
Sigara meridionalis (Wallgr.).
Micronecta scutellaris Stål.
Micronecta piccanin forma *pardina* Hutch.

Of these, *M. piccanin*, though common in the river, has only been found at the head of the canal-like stretch at Station 3 on one occasion, and that just after heavy rains had flooded the river. The others have been found both in the river and in the canal-like stretch, and the two species of *Sigara* have been found on separate occasions at the Ford at the head of the lagoon. The highest salinity at which we have found *S. contortuplicata* and *M. scutellaris* is 7·9°/₀₀, and the highest at which we have found *S. meridionalis* is 19·7°/₀₀.

Order: **TRICHOPTERA.**

Argyrobothrus sp. Larvae common at Station 4.

Leptocerus sp. Larva very similar to that of *L. harrisoni* Brnrd. Station 13, 20/10/48, in brown outgoing water, probably washed downstream.

Order: **LEPIDOPTERA.**

Pyralid larva (similar to that of *Paraponyx* sp.). Station 1, 31/3/48.

Order: **COLEOPTERA.**

Family: **Hydrophilidae.**

Paracymus sp. Station 1, 1/5/47.

Berosus (*S. Str.*) *punctulatus* Boh. Station 5, 1/3/48.

Berosus (*Enoplurus*) sp. nov. Station 5, 1/3/48 and 31/3/48 (common), also in Canal Zone.

Family: **Dytiscidae.**

Herophydrus oscillator Shp. Few at Station 1, 31/3/48.

Herophydrus sp. Common at Station 5, 1/3/48.

Canthyporus navigator Guign. Few at Station 1, 31/3/48, one at Station 12, 1/5/47.

Bidessus (*Guignotus*) n.sp. Common at Station 5, 1/3/48.

Laccophilus lineatus Aubé. Station 1, 31/3/48.

Family: **Haliplidae.**

Haliplus exsecratus Guign. Station 1, 1/5/47, and Station 1, 31/3/48.

Family: **Gyrinidae.**

(KRL 11L, 95A). Stations 1 and 6 (stream mouth).

(KRL 95B, 120). Stations 1 and 6 (stream mouth).

Order: **DIPTERA.**

Family: **Culicidae.**

Culex larvae at Station 1 and in sheltered water at Station 4.

Family: **Chironomidae.**

Chironomus (*Tendiceps*) sp., near *lamprogaster* Kieff. Larvae common all over estuary.

Family: **Simuliidae.**

Larvae of *Simulium* sp., common on stones at Station 1.

Family: **Syrphidae.**

" Rat-Tail " larvae under decaying alga at Station 12.

Class: **Arachnida.**

Sub-class: **Acarina.**

Family: **Eylaidae.**

Small red hydracarines were common at Station 5 in March 1948, and appeared in sheltered positions in the Canal Zone at several times.

Sub-class: **Araneida.**

Spiders under washed-up *Zostera* on beach at Station 9.

Phylum: **ECHINODERMATA.**

Class: **Asteroidea.**

Marthasterias glacialis (L.). Under stones at Station 10 after estuary had been tidal, 11/4/49.

Class: **Echinoidea.**

Parechinus angulosus (Leske). Station 12, in crevice of rocks 1 foot below water, 1/5/47.

Echinocardium cordatum (Pennant).

Specimens of this heart urchin were found over a stretch of about 400 yards from the mouth of the lagoon upwards in the early months of 1949. They were more abundant on the southern shore, but were present for about the same distance along the northern shore. Large numbers had been stranded as the waters receded, but even larger numbers were buried in the sand in the shallows. The burrows were from 1½ to 9 inches deep. Specimens varied considerably in size. Among the larger specimens males and females with ripe gonads were found.

A small depression marked where each *Echinocardium* lay in the sand. The size of the larger specimens suggested that the animals had survived the winter flooding; and further proof was forthcoming, for when the lagoon was opened on 2nd September 1949 several stranded specimens were found.

Phylum: **CHORDATA.**

Sub-Phylum: **UROCHORDA.**

Class: **Ascidiacea.**

Pyura stolonifera (Heller). On rocks at Station 12, from water-level down to 4 feet, 1/5/47.

Solitary simple ascidian (juv.). Rocks at Stations 10 and 11 after estuary had been tidal, 11/4/49.

FISHES.

Sub-Phylum: **VERTEBRATA.**

Class: **Pisces.**

There are very few indigenous fish in the Klein River. The only fish of any size is one which runs up from the estuary, the "springer", *Mugil cephalus* Linn., and this has been reported well above the bridge at Stanford. Smaller fish are the Cape kurper, *Sandelia capensis* (C. and V.), and the small minnow *Galaxias zebratus* Castelnau. Two species of sporting fish have been introduced—the large-mouthed black bass, *Micropterus salmoides* (*Lacépède*), and the spotted bass, *Micropterus punctulatus punctulatus*

(Rafinesque). Both of these breed in the river, and numbers of the former have been seen at Stanford Bridge. They are said to run down into the Canal Zone.

The following species of fish which occur in the estuary have actually been collected and identified:—

Gilchristella aestuarius (Gilch. and Thomp.). Vlei sardine. Inhabit the whole region between Stations 3 and 12, but not, apparently, in large numbers.

Tachysurus feliceps (Valenciennes). Barbel. Common in lower estuary.

Heteromycteris capensis Kaup. Small sole. Common in lower estuary.

Solea bleekeri Boulenger. Small sole. Common in lower estuary.

Syngnathus acus Linn. Pipe fish. Common in the weed from just below Station 5 to the mouth.

Hypacanthus amia (Linn.) syn. *Lichia amia* Linn. Leervis. Present in lower estuary.

Pomatomus saltator (Linn.). Elft. Common in lower estuary.

Rhabdosargus globiceps (Cuv.). White stumpnose. Abundant in lower estuary.

Rhabdosargus tricuspidens Smith. Silver bream. Present in lower estuary.

Diplodus sargus Linn. Dassie. Fairly common in lower estuary.

Lithognathus lithognathus (Cuv.). White steenbras. Common in lower estuary.

Mugil cephalus Linn. Springer. Common throughout whole estuary, to above Station 1.

Liza ramada (Risso) syn. *Mugil capito* Cuv. Mullet. Abundant in lower estuary.

Atherina breviceps Cuv. Silversides, "Smelt". Shoals of these small fish were seen and sampled from Station 4 to the foot of the lagoon. They are quite common all over the lagoon, and at times in the Canal Zone.

Gobius nudiceps Cuv. Goby. Common in lower estuary.

Psammogobius knysnaënsis Smith. Sand goby. Common from Station 5 to the foot of the lagoon, especially in sand.

Clinus superciliosus (Linn.). Klipvis. Common all over the lagoon. Present up to Station 4.

Ophisurus serpens (Linn.). Eel. According to Mr. I. Williams, many of these eels were dug out of the sand which was exposed when the mouth was opened on 3/9/49.

Our observations on the above fishes have been supplemented by information from Mr. F. Talbot of the Zoology Department,* Mr. I. Williams of Hermanus, and Mr. W. Selkirk and Mr. O. Prillevitz, two well-known Hermanus anglers. The two latter have also reported the occurrence of several other marine fish, which we have not ourselves taken. These are: Kob (*Sciaena hololepidota* Lacépède), common; geelbeek (*Atractoscion aequidens* (Cuvier)), present; wildepaard (*Diplodus trifasciatus* (Rafinesque)) and gurnard (*Trigla* sp.), rare. Also occasional sharks, namely Vaalhaai and sand-sharks (*Rhinobatos* sp.), and skates. Kob up to 20 lb. in weight have been taken, but none of the fish has the firm texture of fish taken in the open sea.

Large numbers of fish migrate after the seasonal opening of the lagoon, and various species enter with the tide during this period.

Gut Contents and Gonads.

Examination of the guts of juvenile *L. lithognathus* (3 to 4 inches) showed that they contained predominantly the Talitrid *Talorchestia australis*, with a few mysids; one small *Callianassa kraussii* was found. Juvenile *Rhabdosargus globiceps* contained mostly filamentous algae but also a few mysids. The guts of young *Liza ramada* contained mud and diatom remains.

An examination of the guts of a number of fish sent to us by Mr. I. Williams of Hermanus, which were collected from July to September 1949, gave the following results:—

17 barbel (*T. feliceps*) contained one or more of the following: *Hymenosoma orbiculare, Callianassa kraussii, Leander pacificus* and *Modiola capensis*. (The gonads of all these fish were undeveloped.) 8 white steenbras (*L. lithognathus*), from 8 to 18 inches in length, contained one or more of the following: *Lumbriconereis* sp., *Modiola capensis*, small unidentified Lamellibranchs, *Hymenosoma orbiculare*, and filamentous algae. (The gonads were all undeveloped.) 5 white stumpnose (*R. globiceps*), from 5 to 6 inches long, contained: *Assiminea* sp., *Callianassa kraussii, Echinocardium* sp. 6 silvies (*R. tricuspidens*), 7 to 9 inches long, contained: *Echinocardium* sp., filamentous algae, and bits of *Zostera*. (The gonads were all small except those of a 9-inch specimen, taken on 9/9/49, which were ripe.)

It is to be noted that *Callianassa kraussii* is often used as bait in this

*In addition to those fish mentioned in the list of fauna, we have since been given some further records of fish netted in the lagoon during 1950 and 1951 by Mr. F. Talbot. These are: *Rhinobatos annulatus* Muller and Henle, sand shark; *Pomadasys olivaceum* Day, rock grunter; *Diplodus trifasciatus* (Rafinesque), wildeperd; *Lithognathus mormyrus* (Linn.), sand steenbras; *Sarpa salpa* (Linn.), mooi nooitjie; *Spondyliosoma emarginatum* (Cuvier), steentjie; *Trigla capensis* (Cuvier), gurnard; *Amblyrhynchotes honkenii* (Bloch), toby.

estuary, so that its presence in the gut may not mean that it was caught naturally. However, though most of the fish only contained one specimen, one barbel contained three. One *L. lithognathus* caught in a net contained a small specimen.

BIRDS.

Many years ago the lagoon abounded with birds (pelicans, flamingoes, duck and many different waders), but owing to wholesale slaughter and considerable disturbance the bird population is now comparatively small. Nevertheless, various birds are of interest and also of some importance in the estuary, since they feed on either the weed or the animal life, or scavenge.

These birds fall into several different categories.

A. **Birds of the Mud-flats and Sand-banks.**

Large expanses of mud and muddy sand are exposed or submerged under a few inches of water during the summer and autumn months; these would seem to be ideal haunts for waders, yet comparatively few have been seen. Those observed include small flocks of Sanderling (*Crocethia alba* (Pallas)); also scattered Greenshank (*Tringa nebularia* (Gunn)) and common Sandpipers (*Actitis hypoleucos* (Linn.))—the latter two are common throughout the summer months. The Greenshank occur in small flocks early in the summer, and later are encountered singly, which agrees with the report of Broekhuysen and Meiklejohn (1941) that migratory birds remain in flocks for some time after arrival and then disperse. Curlew (*Numenius arquata arquata* (Linn.)) are also numerous in summer. In addition two indigenous sand-plovers, the White-fronted (*Charadrius marginatus marginatus* Vieill.) and Kittlitz's (*Charadrius pecuarius pecuarius* Temm.), are common round the shores of the lagoon; another, the Three-banded Plover (*Charadrius tricollaris tricollaris* Vieill.), has also been seen.

The European migratory waders mentioned above are known to feed on small animals such as worms, crustacea, small molluscs, etc.

B. **Birds of the Weed Beds.**

In the shallow weed beds along the channel and the margins of the lagoon there are always a few birds to be seen. These include Herons (*Ardea cinerea cinerea* Linn. and *Ardea melanocephala* Vig. and Childr.), of which the former is the more abundant; Hamerkop (*Scopus umbretta bannermani* C. Grant); Egrets (*Egretta garzetta garzetta* (Linn.), *Bubulcus ibis* (Linn.) and *Mesophoyx intermedius brachyrhynchus* (Brehm)); a few Great-crested Grebe (*Podiceps cristatus infuscatus* Salvad.); and, very rarely, a flock of Flamingoes (probably *Phoenicopterus ruber antiquorum* Temm.).

Yellow-billed Duck (*Anas undulata undulata* Dubois) are common throughout the length of the lagoon, particularly in the late autumn and winter months, when flocks of several hundred have been seen.

C. Fish-eaters, Shell-fish Eaters, and Scavengers.

Near the foot of the lagoon large parties of tern and some gulls are usually to be seen resting on the sandy island or the seaward margins of the lagoon. The gulls are chiefly the Southern Black-backed (*Larus dominicanus* Licht.), with a few Hartlaub's Gulls (*Larus hartlaubi* (Bruch.)). The tern vary in species according to the season. In the summer months the flocks are very large, including several thousand birds, and consist mainly of Common Tern (*Sterna hirundo* Linn.) and/or Arctic Tern (*Sterna macrura* Naum.), which are not then in breeding plumage and so are indistinguishable. In addition there are numbers of Crested (Swift) Tern (*Sterna bergii bergii* Licht.), Sandwich Tern (*Sterna sandvicensis sandvicensis* Lath.), and Damara Tern (*Sterna balaenarum Strickl.*), and a few Caspian Tern (*Hydroprogne caspia* (Pallas)).

In the late autumn and winter months most of the migratory terns have left for their breeding quarters, so that the flocks are much smaller.

The Tern do not appear to feed in the estuary to any great extent, going out to sea as a rule, but as they roost on the sand-banks for a large part of their time they add a considerable amount of fertiliser to the lagoon, whose banks are inundated when the water is high.

Other fish-eaters, which usually do feed in the estuary, include White-breasted Cormorants (*Phalacrocorax carbo lucidus* (Licht.)) and Reed Duiker (*Phalacrocorax africanus africanus* (Gmel.)), both common; and occasional Kingfishers (*Ceryle rudis rudis* (Linn.), *Megaceryle maxima maxima* (Pall.), and *Corythornis cristata cristata* (Pall.)).

A small party of Oyster-Catchers (*Haematopus moquini* Bp.) is also frequently to be seen.

D. Birds of Prey.

These include another fish-eater, the Sea-Eagle (*Cuncuma vocifer* (Daud.)), which has been observed on several occasions, and the Marsh Harrier (*Circus aeruginosus ranivorus* (Daud.)), seen circling above the reed beds and salt-marshes.

E. Swallows, Swifts and Rock Martins.

These hawk for insects above the lagoon, catching many Diptera which have aquatic larvae. Various species are present, of which the European Swallow (*Hirundo rustica rustica* Linn.) is by far the commonest.

IX. Discussion.

An estuary has been described as "that area in a river in which tidal effects are evident", but this definition requires extension. In his introduction to the series of surveys of South African Estuaries, of which this is the second paper to be published, Professor J. H. Day has defined estuaries as "the parts of river systems where there is an appreciable variation in salinity due to the sea". This definition indicates that the salinity typically derives from the sea. The movement of salt water into or up an estuary may be due to one or more factors; of these the most important is tidal influence, though seepage through a sand-bar and wind and other currents may also be concerned.

The estuary of the Klein River is for the greater part of each year closed by a sand-bar, and is under tidal influence only for a short period of a few months. This seasonal opening and closing has quite considerable effects on the physical and chemical conditions in the estuary and, as a result, on the fauna. The area studied, as has already been mentioned, can be divided naturally into three main sections, the river, the canal-like stretch and the lagoon, of which the last two constitute the estuary. So far as we have seen only the lagoon shows a tidal rise and fall, although the canal-like stretch is also under saline influence.

While the lagoon is open to the sea, the expected horizontal salinity gradient of an estuary develops, as has already been shown, and this persists as long as there is any tidal influence. The mouth remains open as long as the outflow of water from the river and mountain streams is sufficient to wash away the sand deposited in the mouth by the long-shore currents. As soon as the flow of water from the river becomes insufficient to remove this sand the bar is gradually built up, and as it increases in size, the period of each day during which the estuary is under tidal influence, and the tidal range within the lagoon, will also decrease. This process goes on until only the highest spring-tides come over the bar, and eventually even these are no longer able to cross, and then the estuary ceases to be tidal. So long as the general level of water in the lagoon is lower than that in the sea there is some seepage of sea-water through the bar, and runnels have been seen to develop on the lagoonward side of the bar.

A mass of water is thus enclosed, the salinity of which varies with certain conditions. If the bar be formed early in the season while the river and streams are still flowing strongly, as in October 1947, the water enclosed is of comparatively low salinity. If the bar be formed late in the season when the inflow of fresh water is reduced, as in February 1949, the mass of water enclosed is of higher salinity. After closing the level rises slightly, and wind currents in the shallow basin cause a mixing of the water

and the salinity gradient almost disappears. If the level be sufficiently high some of this water is blown up into the canal-like stretch and so brings it under saline influence, even though it has not shown any tidal rise or fall.

As the summer proceeds and the inflow is reduced to a minimum, evaporation increases the salinity in the broad shallow lagoon, particularly in the lower reaches where the shallows are more extensive, and so again a horizontal salinity gradient is set up. The prevailing south-easters blowing down the lagoon encourage its development. In autumn, when the rains come, north-westers tend to eliminate the salinity gradient. The streams and river begin to flow again and fill up the lagoon with fresh water, and the salinity as a whole decreases. When the level is high enough to flood surrounding farm lands, the mouth is cut and the estuary opened to the sea, once more becoming tidal.

Physical factors, such as hydrogen-ion concentration and temperature, do not vary sufficiently to have any influence on the fauna. Unlike many South African estuaries this particular one has almost no turbidity, for soil erosion in this district is not so extreme as in other catchment areas. Suspended matter is only noticeable in the upper reaches.

Animals which live in an estuary of this sort must be able to withstand daily changes in salinity while the lagoon is tidal and also seasonal changes while it is closed.

In his introductory paper Professor Day has enumerated five components into which it is possible to fit the animals found in an estuary. Each of these will be discussed in turn in relation to the conditions in this particular estuary.

(*a*) **The Freshwater Component.**—The animals, chiefly aquatic insects, which can be included in this component normally live in fresh water but have a certain degree of salt tolerance. Usually they are to be found only in regions of low salinity (less than $8°/_{oo}$). Some of them, *e.g.* naiads of *Cloeon* sp., and the Corixid, *Sigara meridionalis*, have, however, been found in a salinity of $19{\cdot}7°/_{oo}$ and so can withstand salinities at least as high as this. In the Klein River estuary these animals are restricted to the canal-like stretch and to the ford at the head of the lagoon.

(*b*) **The Stenohaline Marine Component.**—This comprises those animals which enter the estuary from the sea while the lagoon is open. Some of these, such as the amphipod *Paramoera capensis*, have only been found on an incoming tide and apparently do not establish themselves in the estuary at all. Intertidal forms, such as *Littorina knysnaënsis*, *Oxystele* spp., *Siphonaria* sp., and other more or less sedentary types, colonise rocky outcrops and large stones at the foot of the lagoon, but many individuals die during the winter floods, the number dying depending on the amount

of dilution. During a very wet winter all may be killed off. Others again, like *Ovalipes trimaculatus*, *Echinocardium cordatum* and *Arenicola loveni*, only establish themselves near the mouth, and survive the winter if the salinity does not fall too much.

(*c*) **The Euryhaline Marine Component.**—All the marine organisms which establish themselves for any length of time in the estuary and which breed there would fall into this category. The variety of their tolerance of salinity range is, however, considerable. Some forms, such as the sand-prawn *Callianassa kraussi* and the shrimp *Leander pacificus*, seem equally at home at all seasons and throughout most of the lagoon, and both have been found breeding.

Intertidal forms, such as *Deto echinata* and *Ligia dilatata*, *Talorchestia australis* and *Cyclograpsus punctatus*, have a considerable tolerance, and in all the seasons studied have survived the winter flooding. These animals occur on or just above the water-level, and thus maintain their usual position on the shore. *Solen capensis*, although only to be found at the foot of the lagoon, occurs in backwaters where the salinity may be low for some time (13°/₀₀ at Station 12).

(*d*) **The Estuarine Component.**—Into this category we have put those organisms which are restricted to estuaries or which seemed to us to prefer the estuarine habitat to that of the sea. It is often difficult to decide whether a particular organism belongs to this or to the euryhaline marine component, because our knowledge of distribution is incomplete and we do not know the extent to which some animals live in the sea.

In European estuaries there is a horizontal zonation of species of *Gammarus* throughout the length of an estuary. No comparable zonation has been found here, with one exception. Two Sphaeromid isopods are abundant in the estuary, but each forms a separate community and the two species do not overlap. *Pseudosphaeroma barnardi* is restricted to the area where fresh and brackish waters intermingle—*i.e.* in the canal-like stretch and at the mouths of the mountain streams. *Exosphaeroma hylecoetes* abounds in the lagoon.

Amphipods and tanaids are important members of this component, and each species tends to have a predilection for a certain type of substratum on which it is abundant and to which it is virtually restricted. For example, the tanaid *Leptochelia savignyi* inhabits all the mud-beds throughout the estuary, whether these be clothed with weeds or not. A tiny amphipod, *Grandidierella lutosa*, makes its minute holes in the surface inch or so of muddy sand. *Corophium triaenonyx* attaches little mud tubes wherever it finds a solid substratum. *Parorchestia rectipalma* swims around among the stones of gravel beds or among the reeds or rushes where these are surrounded by water. *Talorchestia ancheidos* is the common sandhopper

on gravelly beaches. *Hymenosoma orbiculare*, a little crab, has been found on sandy bottoms and weed beds throughout the length of the lagoon, and its zöaeae in the plankton even of the canal-like stretch. *Modiola capensis*, a small mussel, and a tiny snail, *Assiminea* sp., are also present throughout the length of the estuary often in very large numbers.

(*e*) **Migratory Component.**—Many of the fish which are found in the lagoon come into this category.

The position of the mouth and the extent and length of time which it is open seem to influence the fauna quite considerably. As one would expect, it is the euryhaline marine component which is affected. In 1948 the mouth was open from September to February, and most of this time was deep and the tidal current strong. During this season the variety of species and number of individuals introduced into the lagoon was large. In 1947 the mouth was only open from July to November, and from September onwards was shallow and the tidal effect slight. During this season very few marine forms established themselves.

In 1946 the mouth was cut near the Hermanus end of the bar and marine communities developed on the adjacent rocks at Station 12. Most of these animals died in the following winter, and none survived two winters. In 1947 and 1948 the mouth was cut at the opposite end of the bar and marine communities were established at Stations 11 and 10 (*i.e.* those rocks nearest to the mouth past which the tide flowed). No animals established themselves at Station 12, which was then in a backwater.

In 1949 the mouth was opened between these two extremes opposite a large sand-bank, and remained open from September to November. The level rose again and the lagoon was reopened in December. Many marine organisms survived the winter of 1949, for the water during this season retained a high salinity, but it is not expected that many new individuals were introduced, because the tidal influence was slight and a twice-daily range only noticeable at the foot of the estuary.

As a result of these observations it appears that the establishment of marine communities in the lagoon depends on the extent of the tidal influence, for such communities are only established in suitable localities which are washed by the tidal current.

The seashore animals which become established in the lagoon show signs of the same zonation as has been described on the shore (Stephenson, 1939, 1944, 1947; Stephenson and Stephenson, 1949). The Supralittoral fringe, with *Littorina knysnaënsis* and *Oxystele variegata*, and the Infralittoral fringe, with *Pyura*, can sometimes be distinguished. It is the Midlittoral zone which becomes very much foreshortened, the animals (e.g. *Oxystele tigrina* and barnacles) occupying a very narrow strip along the water-line. This foreshortening is presumably due to the fact that tidal action is slight

or absent. Stephenson and Stephenson (1949) discuss this type of zonation and its causes where there is no tidal change.

X. Summary.

This is a survey of the Klein River Estuary, near Hermanus, Cape, in the Western Cape Winter Rainfall Area. The estuary lies in a small coastal plain beneath a range of mountains composed mainly of Table Mountain Sandstone. There is a description of the topography and the physical and chemical conditions; the estuary is usually closed to the sea for most of the dry season; it is always more or less saline; the water supply is acid though the estuarine water is alkaline; suspended matter settles rapidly and is relatively unimportant.

Some mention is made of the relevant flora.

The main section of the paper deals with the ecology of the fauna (mostly bottom fauna), from the lower freshwater reaches of the river through the increasingly saline waters of the estuary to the mouth. Some attempt is made to relate the fauna to the substratum. There is a faunistic list and a series of biological notes on individual species.

The discussion deals with the relationship of the biota to the seasonal opening of the mouth and influx of fresh water with the consequent fluctuations of salinity. An attempt is made to indicate the derivation of different faunistic components.

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The Canal Zone near Station 4. Taken when the water-level was very high.

The Northern Shore. Looking across the lagoon from near the boathouse towards Station 10 (extreme right). Water-level high.

The Channel. Looking down the lagoon from above Station 10 (right foreground) to the mouth. The water-level was low; the mouth was open. The sand-bar between lagoon and sea can be seen in the distance.

Weed beds in shallow water in the lagoon. Looking across from near the boathouse to Station 11. The main part of the lagoon is just visible beyond Station 11. The water-level was very low when the photograph was taken.

THE EVOLUTION OF THE MIDDLE UGAB VALLEY, DAMARALAND, SOUTH WEST AFRICA.

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(With Plates XXVII–XXX and 7 Text-figures.)

(Read June 21, 1950.)

Abstract.

This paper attempts to reconstruct the regional history of uplift and climate since the Cretaceous from the terrace deposits and equivalent features in the Middle Ugab Valley, and from their relationship to adjacent erosion surfaces.

Pre-Karroo planation was not advanced, but by earliest Tertiary times the "African" Surface, with characteristic inselberge, had been formed. This surface is preserved on the divide to the south and as a summit plane north of the Ugab, although modified by Tertiary warping along the Otavi axis. The pre-Middle Eocene Ugab occupied a broad valley on this surface.

Within the valley three levels are recognised. The Main Terrace surface lies 500 feet above the present river and contains up to 300 feet of sands and conglomerates capped by calcareous sandstones and resting on a weathered Eocene ("Pedestal") surface. These deposits indicate aridity during the Tertiary period. Their dissection followed upon end-Tertiary uplift with a semi-arid climate and produced the Lower Terrace, 100 feet above river-level. This is mainly erosional, but equivalent deposits downstream have been dated from artefacts as Lower and Middle Pleistocene. An Upper Pleistocene wet phase caused erosion below the present flood-plain followed by the deposition of a sandy alluvium with Middle Stone Age tools. This is now undergoing dissection into a lowermost terrace.

CONTENTS.

A. Physical Setting.

1. *Regional Drainage.*

From its source on the Damaraland Plateau in latitude 19 deg. 50 min. S., the Ugab River follows an almost direct W.S.W. course to the sea. Although the valley has on physical grounds been included in the Kaokoveld (Maack, 1923), it differs to an important degree from the drainage to the north.

In this latitude the watershed of the seaward drainage of South West Africa, elsewhere formed by the western margin of the plateau, is pushed farthest back into the interior; the Kalahari divide is sharpened, and less than 30 miles separates the Ugab headwaters from the Kalahari Sands. This deep embayment corresponds to the region of highest rainfall in South West Africa, running from the Khomas Highlands north-east to the Otavi Mts., and the greater erosive power of the Ugab, Omaruru, Khan and Swakop Rivers is reflected in a regrading of the plateau edge. "In Western Damaraland the Great Escarpment terminates at the north-west buttress of the Khomas Highlands, south of Otjimbingwe. In the region of the bigger rivers the Great Escarpment has been dissected almost beyond recognition" (Gevers, 1936). Coastal plain and interior plateau here pass imperceptibly one into the other, with a transitional belt of marked valley incision by the most competent drainage of South West Africa.

Evidence has been brought to show that this embayment is not wholly erosional in origin. An erosion surface at 6180–6500 feet on the Khomas Highlands is continued northwards with a gradual descent as a summit plane across the dissected inselberg region of Western Damaraland, indicating transverse flexuring along the north-eastwardly directed Khomas Axis, superimposed on the Tertiary uplift of the continent. "These four rivers, responsible for this intense dissection . . . are situated comparatively close together, and can be considered as flowing in an original, shallow down-warped trough of the Khomas peneplain" (Gevers, 1936). Korn and Martin (1937) have suggested that the ancient, south-west–north-east striking fold-structures of Damaraland intercepted the recent marginal flexure, and that a Tertiary drainage has persisted across the original surface, tilted and warped only to a comparatively minor degree.

Despite their achievement in erosion, these streams are typical South West African "Reviere", coming down only after heavy rain, progressively becoming lost in and choked by their infilling of sand, and reaching the sea only once or twice in a decade. Otherwise they appear as shallow, braiding channels, often a few hundred yards in width and filled to varying depths with gravel, grit, and sand. Their gradients are steep compared with those of perennial streams. The Swakop River falls 1307 metres in

307 kilometres, and the measured gradients of the Ugab River are similarly between 1 in 200 and 1 in 300, a rate of fall 10 times that of the Main. However, the ability occasionally to flush their channels clear of accumulated debris distinguishes the rivers of the Northern Namib from those further south, and is associated with an effective down-grading towards sea-level which stamps the drainage system as "semi-arid" from a physiographical point of view (Cotton, 1942).

2. *The Sub-Regions of the Ugab Valley.*

Within the area drained by the Ugab, and trending at right angles to its course, four morphological divisions can be recognised, in each of which the main valley assumes a characteristic form.

(a) *The Namib Coastal Plain.*—This marginal plain, up to 90 miles in width, was developed by subaerial erosion under more humid conditions during the late Cretaceous. Subsequently it has undergone intermittent outward tilting and rejuvenation, associated with the rise of the subcontinent, culminating in the differential uplift of Upper Tertiary-Pleistocene age evidenced by the coastal terraces. The plain rises steeply inland with an average gradient of 1 in 100. Where it is bounded by the Great Escarpment the Namib may reach an altitude of 1000–1300 metres above sea-level. The marginal flexuring is shown in a slight convexity of transverse profile and a progressive incision of drainage towards the interior.

A mantle of sand, surface limestone, and the rock waste peculiar to arid regions covers the lower ground, masking its irregularities, and exposures of bare rock are limited. In the last four miles of its course the sand-filled river bed occupies a wide, shallow depression in this waste-covered plain. Eastwards, however, the valley is lowered to an increasing depth beneath the general surface while relief is further diversified by occasional residual "inselberge", rising abruptly from their own debris.

(b) *The Transitional Plains.*—There is no physical break between the Namib surface and its continuation, north and south of the river, into the Transitional Plains. From the interfluves the same surface falls valleywards with slightly convex slopes. Above the Plains, with their widespread cover of surface limestone, rises the most spectacular of the inselberge, the geologically youthful Brandberg (2606 m.). The position of the highest peak in South West Africa within the heart of the Ugab Valley is indicative of the small part played by these scattered residuals in the delimitation of drainage systems.

The incised character of the valley below Tsawichaams to a point 40 miles beyond the Brandberg entitles this region to separate treatment, despite the lack of sharply defined limits.

In the "Ugabschiefergebirge", west and north-west of the Brandberg, the valley assumes a true gorge form. The area has been described by Cloos (1931). The erosion surface south of the Ugab is continued northwards in the summit plane of these highly dissected schist hills. Approximately 100 metres below this level is developed a broad, winding valley-floor plain (Trogfläche), into which the river has cut down, between almost vertical rock walls, to a depth of 100–150 metres. Narrow, winding gorges bring in the similarly incised tributaries. In a second infolded belt of schists traversed by the Uis River, 30 miles to the south-east, the Uisberge show an advanced stage of valley dissection. Between Sorris-Sorris and the Brandberg, in its course across granite country, the main valley is somewhat less deeply entrenched, while the Trogfläche is here represented by rock-terrace remnants 150 metres above the river bed. In the schists above Sorris-Sorris the Ugab and its tributaries again display sharp incision, as in the hilly country upstream from Otjondu (fig. 4), but above Oresuwa the valley opens gradually until Tsawichaams is passed, when gently rolling surfaces and extensive tributary plains form the transition from the broad main valley southwards to the interfluvial surface in the Otjohorongo Reserve.

(c) *The Central Hereroland Plateau.*—Since a detailed analysis of this region forms the main subject-matter of the article, only the salient features will be noted here. At an altitude of approximately 1000 metres above sea-level, the rate of ascent of the Plains towards the interior falls off, and with it the degree of drainage incision. In strong contrast to the Omaruru River, which is only slightly lowered into the adjoining country, the Ugab here occupies a broad valley, 2 or 3 miles wide and 500–600 feet below the level of the surrounding Plateau, while remnants of a Tertiary valley-fill form an impressive terrace. Northwards, the valley abuts sharply against limestone hills, outliers of the Franzfontein Mts.;* to the south, gently undulating schist country leads to the Ugab–Omaruru divide.

(d) *The Watershed.*—North of the Ugab the Franzfontein Ranges pass gradually into the Otavi Mts., which elsewhere rise sharply from the Plateau at 1400–1450 metres. South of the valley, near Otjiwarongo, the inselberg landscape of Central Hereroland passes into a region of low hills where "the basement rocks, low ridges of crystalline limestones, disappear under a widespread cover of surface limestones and sands (Range, 1929). Fig. 1, B shows the extent of this surface deposit—more or less sandy limestones, calc-breccias and reddish sands—which may be several metres thick, and may be regarded as an extension westwards, across the watershed, of the Kalahari deposits of the Sandveld. Despite what is, for South West

* The Nama word Ugab is translated as "a river running close to and deep among mountains" (Maack, 1923).

Africa, a heavy rainfall, surface drainage becomes disorganised and in places completely lacking by virtue of the porosity of these surface deposits, the lack of regional slope, and the demands of a thick vegetation. The Ugab Valley forms a featureless limestone plain with no stream bed, and the valley-fill, here exceeding 100 feet in thickness, remains completely undissected.

3. *Climate and Vegetation.*

It has been of fundamental importance in the recent geological history of the Ugab Valley that the strike of the Damara sediments, and with it the course of the river, lies at right angles to the trend of the isohyets (fig. 1, A). The physiographical divisions outlined above accordingly correspond in some degree to distinct rainfall provinces.

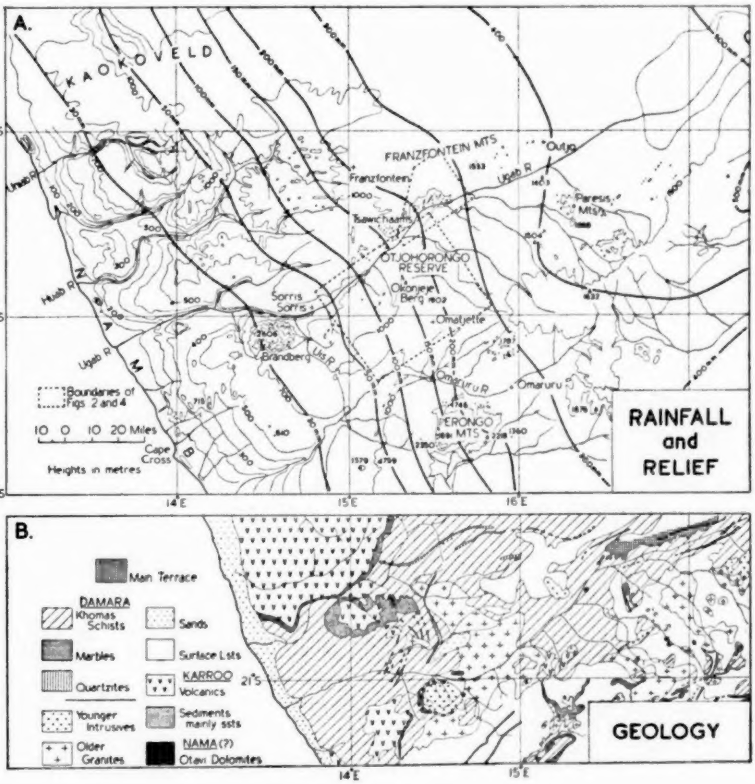


Fig. 1.

West of the Brandberg the Namib is true desert. The average annual precipitation at Swakopmund over a period of twenty years is 0·63 inch. The rainfall is episodic, and the specialised plant life is more dependent on the frequent heavy mists.

The Plains to the east form an area of unreliable periodic rainfall, 30–100 mm. being an average annual total. They comprise a transitional Euphorbia zone followed eastwards by extensive shrub-steppe, with zones of thicker vegetation in the moister river gravels and on the hills.

On the Hereroland Plateau the rainy season lasts from November to March, and the precipitation ranges from 100–400 mm. The characteristic vegetation is tree-steppe, replaced by bush-steppe on the extensive surface limestones. Within this section of the Ugab Valley the mopane is widespread and indicates the transition towards the Kaokoveld. On the limestone hills it is progressively replaced by the kokerboom (*Aloe dichotoma*) and thorn trees, while the river bed is marked by a corridor of closer vegetation with large trees.

Only the watershed region, with a more dependable annual rainfall of over 400 mm., can be described as semi-arid. Even here the lack of surface water imposes a drier stamp upon a vegetation consisting of dense thorn-tree steppe, with widespread grass cover after the rainy season.

Table I.—Geology.

Recent Deposits.	Sand, Surface Limestones and Alluvium.	
Tertiary (?)	Main Terrace deposits of the Ugab River	
Karroo System	Dykes and lava flows Sediments (Otjongundu Plateau)	
	Unconformity	
Nama System (?)	Otavi Dolomites	
	Unconformity	
Older Granites (Intrusive into the Damara System)	Later phases of granite intrusion Salem Granite	Fundamental Complex
Damara System	Khomas Series Marble Series	

If we seek to equate these rainfall provinces with the sub-divisions of arid climates proposed by Kaiser (1926), the Namib becomes "extreme-arid", the Transitional Plains "normal-arid", and the Watershed "semi-arid". The climate of the Central Hereroland Plateau and Ugab Valley, in the area to be described in detail, is transitional from "normal-" to "semi-arid". Its position, therefore, is a critical one in an examination of the history of the Ugab Valley, since "districts in which climatic oscillations will be most apparent are those lying along the edges of the arid belt" (Maufe, 1935). In such areas a comparatively small increase or decrease in rainfall may bring about important changes in the balance between accumulation and fluviatile transport.

B. The Geology of the Area.*

The overall geology is shown in fig. 1, B, while the formations in the area under review are set out in Table I.

The Damara System.

(a) *The Marble Series.*—Thin marble bands occur at numerous levels within the Damara System, but are especially concentrated in this zone, marked by at least one bed of massive crystalline limestone frequently over 1000 feet thick. With the gradual disappearance of the basal Quartzite Series north of the Swakop River the marbles play an increasingly important rôle as relief makers, generally forming elongated ridges or even high mountains along the crests of anticlines. In part this reflects a northwards increase in the thickness of the Series, in part the closeness of the folding. The Marble Series achieves its greatest development just beyond the southern limits of our area.

The more highly metamorphosed forms disintegrate on weathering into rhombohedra of calcite, and give rise to low whitish hills, as between Omatjette and the Otjongundu Plateau. The less metamorphosed, finer-grained, blue-grey limestones are more common. These form hills of darker colour, and usually show strong solution weathering—the rough, fluted surfaces known as "olifants klip", solution cavities, and extensive areas of true "karrenfeld".

(b) *The Khomas Series.*—The Marble Series is followed conformably by an immense thickness of mica-schists with every gradation to micaceous quartzites. Dull silver-grey when fresh, they weather loose and take on a

* Information has been drawn in particular from Cloos (1919, 1931), Gevers and Frommurze (1929), Gevers (1934), and Geological Survey, Sheet 71 (Omaruru, S.W.A.), with accompanying explanation.

brownish tinge, generally imparting a sombre aspect to the countryside. On the Ugab–Omaruru divide they outcrop in thin strips, sandwiched between granite bodies, but north and east of the Otjongundu Plateau they are extensively developed, and cover the whole area as far as the Ugab River.

Here they give rise to rolling country with numerous flat-topped hills and wide river-plains. Run-off across the schist slopes is high, resulting in dissection by a close network of channels, while the consequent lack of ground-water is reflected in the scarcity of trees. The relief shows a large measure of structural control, despite its unspectacular nature. Lines of hills mark the quartzitic horizons or the numerous quartz veins, and the hills themselves are characteristically arranged *en échelon*, separated by deep transverse valleys developed along schistosity planes.

Folding.—In pre-Cambrian times the Damara sediments were intensely folded from the south-east, and the regional strike is north-east–south-west. Multi-lateral stresses developed during the period of compression have resulted in—

(i) Local up-domings and down-warpings, the former commonly followed by the intruding granites.

(ii) Sudden changes in strike and rock thickness. This is especially true of the Marble Series, where the irregularity of the folding is seen in the sinuous courses of many limestone ridges.

The Granite Intrusions.—The latter stages of folding were accompanied by granite intrusion on a scale not since repeated in the history of the continent. The main intrusive phase was that of the Salem Granite, a grey, porphyritic, biotite-granite emplaced conformably in phaccolithic bodies mainly within the folded schists. On the plateau south of Omatjette the Salem Granite predominates over the sediments in area of outcrop. In general it is not important morphologically, forming extensive level surfaces partially masked by granite detritus and from which rise occasional exfoliation domes.

Differentiation of the parent magma led to the intrusion of increasingly acid granites during the later phases. A coarse-grained red granite consisting almost entirely of quartz and dark red felspar outcrops extensively within the Ugab Valley below Sorris-Sorris. A non-porphyritic granite, generally intruded marginally to the Salem Granite, is the most widespread of these later types, but much more important physiographically are the compact, resistant aplitic and pegmatitic varieties, which build some of the most prominent inselberge.

The Otavi Dolomites.—Dark-grey dolomitic limestones form sharply-rising hills within and north of the Ugab Valley. They are outliers of the

Franzfontein Mts. and connect laterally with the Otavi Mts. The limestones have been gently folded, together with the Fundamental Complex, on east-west or north-east–south-west axes. The weathering forms are similar to those of the less metamorphosed limestones of the Marble Series, with the widespread development of "olifants klip" on exposed rock surfaces.* Numerous springs issue from the limestones, and the hills, although smooth in outline, are dissected by frequent winding gorges.

Karroo Sediments and Volcanics (*Otjongundu Plateau*).—The sediments form an irregular deposit of feldspathic grits, conglomerates, and interbedded red laminated shales, generally less than 50 feet thick in the east but thickening westwards to as much as 400 feet. They overlie an uneven floor of Salem Granite and schists and have originated as a granite weathering product. In part they have accumulated *in situ*, in part they are fluviatile. Above, the Plateau is capped by sills and flows of a light-brown porphyrite to a total thickness of 400–500 feet. North-eastwards the volcanics abut against the related Okenjeje igneous complex.

The sediments and lavas form a close parallel to the succession in the Erongo Mts., and it has been suggested that in late Karroo time a continuous volcanic cover extended westwards to the latter area and north-westwards to the Brandberg and beyond. Against this must be set the improbability that so much material could have been removed by post-Karroo erosion, leaving no trace behind.† This fact, and the observed relationships of the volcanic rocks on the Otjongundu Plateau and the Okenjeje complex, make the concept of separate central volcanoes a more likely one. The probable identity with the Kaoko sandstones and lavas renders a Stormberg age likely.

This plateau feature is more characteristic of the area north of the Ugab and can be regarded physiographically as a southern outlier of the Kaokoveld.

Recent Surface Deposits.—Thin sand deposits are found extensively over outcrops of the parent granite and everywhere fill the dry stream beds. Surface limestones are especially developed on the southern half of the Otjohorongo Reserve and among the hills north of the Ugab. Eastwards they increase in extent, closing in on the valley from both sides and passing into the Sandveld. Lithologically they vary from pure, grey-white, nodular limestones to brownish calcareous sandstones. The deposits overlie an uneven rock surface, often to a depth of some metres, and are overlain in

* The unconformable contact between the Otavi and Damara rocks is denied by some authorities, who regard the Otavi Limestones as identical with the Damara Marbles.

† Cloos (1931) has estimated that the younger intrusives of the Erongo and Brandberg complexes must have been emplaced beneath a porphyrite cover 500 to 600 metres in thickness.

turn by sand or fragmentary secondary limestones. Where they are well developed the landscape takes on a monotonous appearance, since surface drainage is restricted and vegetation, particularly tree-growth, is scantier.

C. Terraces and Related Surfaces.

Along the northern flank of the Middle Ugab Valley is developed a terrace, with nearly 300 feet of alluvial fill protected and capped by tabular sandy limestones, the level surface of which lies 500 feet above

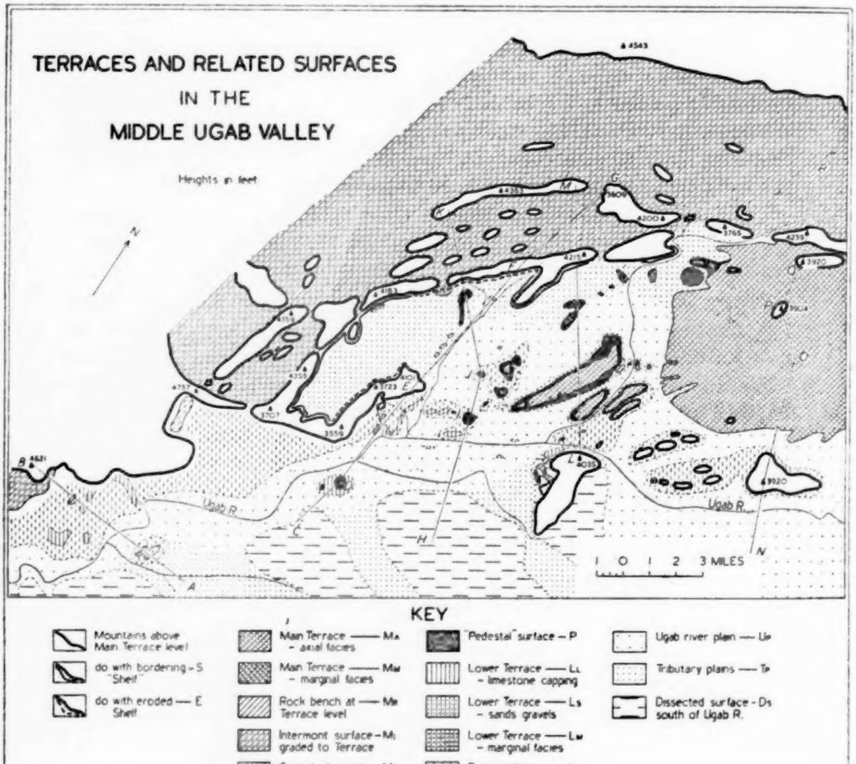
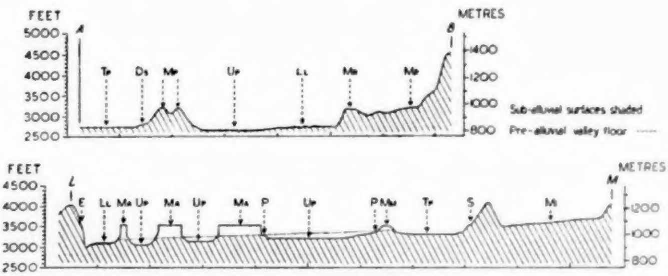


Fig. 2.

river-level. Within our area this terrace ends in a group of "mesas" which yield abundant sectional data. Beneath the sediments and lavas of the Otjongundu Plateau, 35 miles to the south-west, the sub-Karroo

Surface is preserved, and adjacent to it lies the "African" Surface, with its inselberg landscape. This area was therefore chosen for closer field study. A detailed morphological survey was carried out in the valley itself (figs. 2 and 3) and traverses were made across the southern slopes (fig. 4) in order to relate these data to the sub-Karroo and later surfaces.

SECTIONS ACROSS THE MIDDLE UGAB VALLEY



Horizontal distances shown in miles. Vertical exaggeration 4.17 times. Section lines and surface designations as in Fig. 2.

Fig. 3.

1. *Main Terrace Levels.*

The Main Terrace.—The alluvial terrace mentioned above is shown in fig. 2 as the "Main Terrace". Its extent outside the area under immediate study is given in fig. 1, B. It forms a remarkable scenic feature, not only by virtue of its area and its height above river-level, but also on account of the protective capping of sandy limestones and calcareous sandstones, which have given it the name "Kalkterrasse".

Seen from below, the apparent smoothness of the upper surface is deceiving. On ascending, one finds a broken limestone terrain, with numerous solution depressions and occasional steep-sided marginal clefts, densely covered with mopane and thorn-bush. An overall picture is only possible from the hills which rise up through the terrace. From these points a new perspective is obtained, for the present river-plain is lost to view and one sees merely the valley of an earlier period. It extends as a broad, flat depositional feature between the limestone ranges and merges northwards into an "intermont surface", partly depositional and partly erosional though generally bearing the same surface limestone cover. Down-valley, to the limits of visibility, the terrace surface can be projected beyond its eroded margins, across the flat-topped rock benches and spurs which alone survive from this earlier period.

Throughout its length the terrace is practically confined to the north side of the valley. Its survival here is probably due to the bordering dolomite hills which have yielded the limestone matrix of the terrace capping. Further west near the Rotstein (fig. 4), where the dolomites

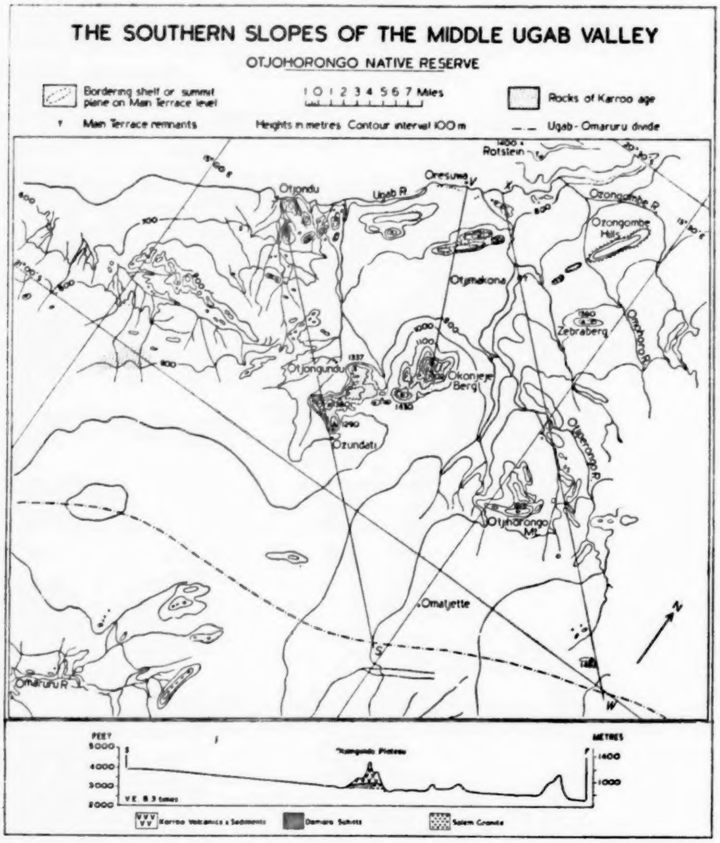


Fig. 4.

give place to the quartz-porphyries of the Summas Mts., the terrace deposits are absent. Significantly also, the terrace remnants south of the Ugab at Pt. D and S.S.W. from Pt. L in fig. 2 are found where limestone hills approach most closely to the river. In former times, in this area, the Main Terrace must have had an equivalent if not greater extent south

of the river. The discovery of a residual fragment near Otjimakona (fig. 4), 7 miles from the Ugab and showing over 100 feet of deposits, strongly supports this view. Presumably the less indurated valley-fill in this southern portion has succumbed more easily to later erosion.

Below the Rotstein, it is unlikely that the Main Terrace was ever developed to the same degree, for the valley-plain narrows towards the incised "transitional" section described above. From fig. 2 it can be seen that the unusually extensive terrace above this point is associated with the curve of the bordering hills, concave to the south, so that the deposits lie in a valley-plain embayment, partly defended by the nodal position of the Rotstein against lateral encroachment northwards by the main stream.

After an unbroken stretch of 50 miles below Outjo (fig. 1, B), the Main Terrace disappears as a depositional feature, first breaking up into the group of "mesas" shown in fig. 2. Present-day erosion of the terrace (including the rock basement as well as the alluvial deposits) takes place in the following ways:

(*a*) Lateral erosion by the main stream during flooding. This is more important upstream from the area shown in fig. 2, where the valley floor abuts directly against the undissected terrace foot.

(*b*) Lateral erosion by tributary streams.

(*c*) Headward sapping by springs emerging at the base of the alluvial deposits. The work of perennial "fonteins" is observable in the deep fretting of the terrace margin shown in the east of fig. 2.

(*d*) Rock-falls due to undermining of the resistant terrace capping through erosion of the softer sands beneath. Aided by the vertical jointing of the surface limestones and cemented sandstones, it leads to the isolation of spectacular "Zeugenberge". The mantle of fallen rock littering the lower slopes of the terrace face shows that this process is everywhere very active.

The "Kalkterrasse" is almost devoid of surface drainage. Few tributaries join the main stream from the north, and such as do exist have probably developed as in (*c*) above. Significantly, the first important right bank tributary received by the Ugab traverses the zone of terrace dissection. Springs are unusually abundant in the adjoining limestone hills, which must have enclosed the original terrace on three sides. Such circumstances would naturally result in excessive spring sapping in this particular area, and to that process the initial stage of erosion of the Main Terrace is ascribed. With the progressive removal of the limestone cover normal tributary drainage can develop. Stream erosion tends to follow strike-lines in the underlying Damara schists (here N.N.E.–S.S.W.), and the majority of the "mesas" are elongated in this direction.

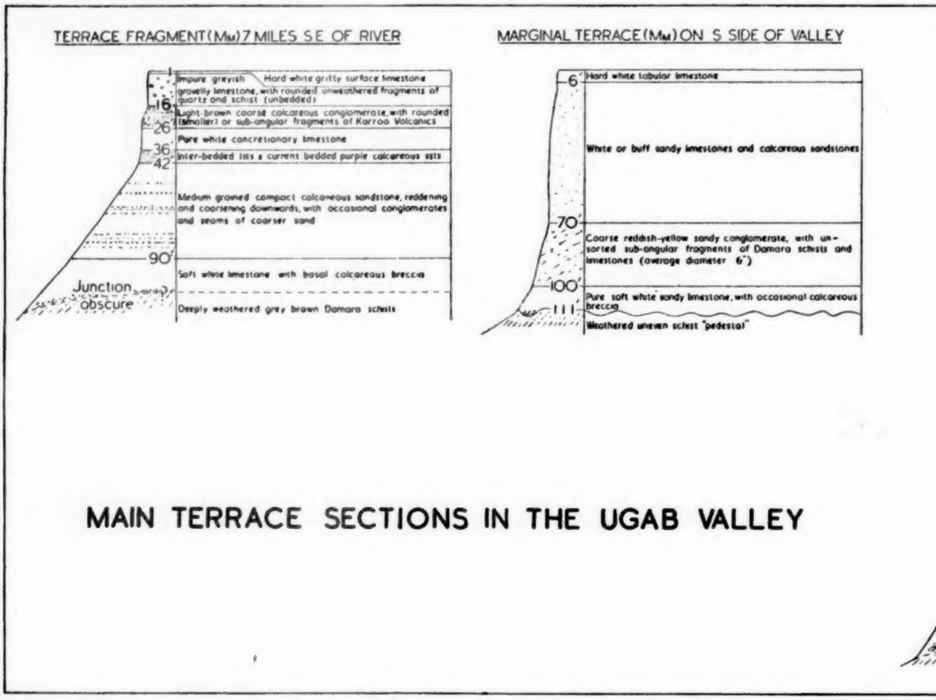
The Main Terrace Sections.—Sections through the Main Terrace show

important differences between the central and marginal portions of the valley, both in the character and thickness of the deposits. Accordingly, "axial" and "marginal" facies have been distinguished, and examples of each are given in fig. 5.

(a) *Axial Facies.*—Within the area studied in detail no significant variation was observed, either in thickness or in the nature of the deposits, along the line of the present valley. The longitudinal gradient of the terrace surface, like that of the present Ugab, is approximately 1 in 300. In the central zone the terrace deposits are almost 300 feet thick. Precise measurement was impossible, for the basal contact, where not obscured, was indeterminate, the recent sediments passing downwards into weathered and similarly calcified Damara schists. Fortunately this pre-alluvial surface often stands out as a marked shoulder beneath the terrace face (Plate XXIX*b*). It has been named the "Pedestal Surface" because of its relationship to the smaller terrace remnants, and in fact it only becomes really obvious during the later stages of dissection.

Generally, the deposits begin with a rubble-bed overlying a deeply weathered schist surface. Both have been more or less calcified. Above lies a great thickness of soft, sandy limestones, which form moderately steep slopes, usually covered with fallen material. Midway through the section follows a layer of uncemented red-brown sands, forming a line of weakness along which undermining of the upper half of the terrace may take place. Some 70 feet of light brown calcareous sandstones follow, with well-defined pebble seams, and horizons of calcified rootlets. These generally form a vertical face. In strong contrast to the well-rounded quartzite pebbles of this horizon are the coarse subangular fragments of the succeeding conglomerates. These consist mainly of local material mixed with sand and firmly lime-cemented. Above the conglomerates the terrace capping shows two horizons. Below is a reddish sandy limestone, through which are scattered occasional pebbles. This passes with decreasing sandiness into whitish surface limestones, which often show secondary silicification.

(b) *Marginal Faciès.*—The deposits thin towards the margins of the valley, and at the same time there is an increase in the amount of coarse, little-rolled, and locally derived rock fragments. Interbedded with these conglomerates are pebble-bearing calcareous sandstones, typical of the axial facies. In the marginal terraces on the section lines J–K and L–M in figs. 2 and 3, coarse, cemented breccias or roughly bedded conglomerates, with fragments up to 18 inches in diameter, were seen to grade into pebble-bearing sandstones towards the centre of the valley. That these conglomerates are the products of erosion of the adjoining dolomite hills is shown by the occurrence there of entirely similar deposits within the present stream channels.



MAIN TERRACE SECTIONS IN THE UGAB VALLEY

FIG. 5

J. A. Mabbutt.

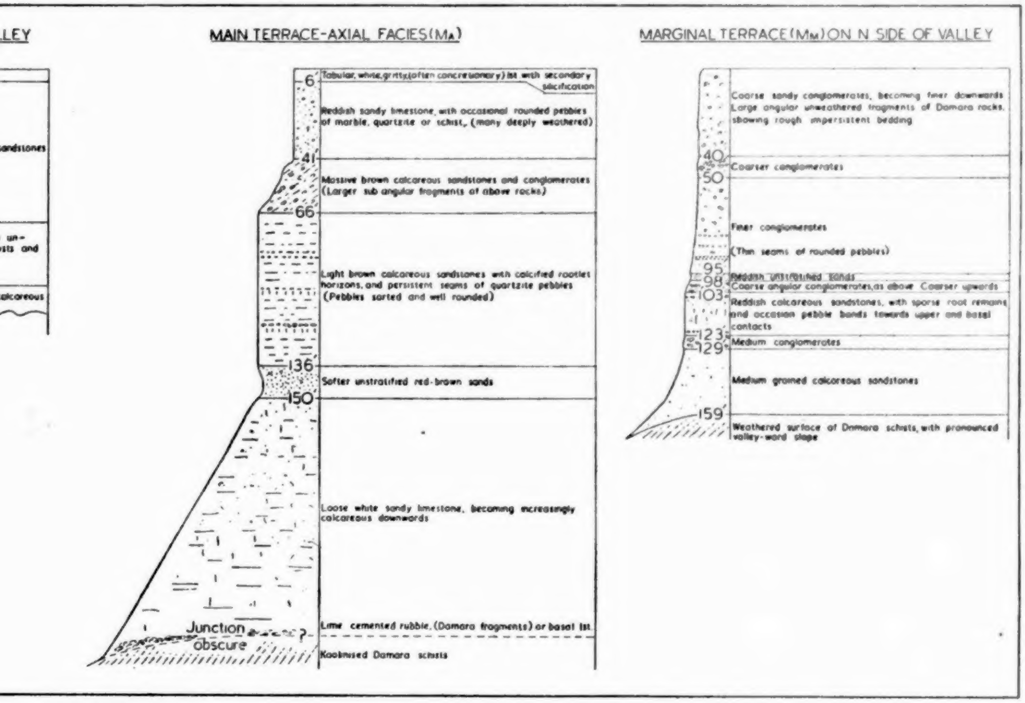


Fig. 5.

[To face page 346.

In the sections south of the Ugab the conglomerates are less developed, and one may assume that the axial facies characterised most of the terrace now removed from that area. The southernmost terrace fragment is of interest in that it includes volcanic material, presumably derived from Okenjeje Mt.

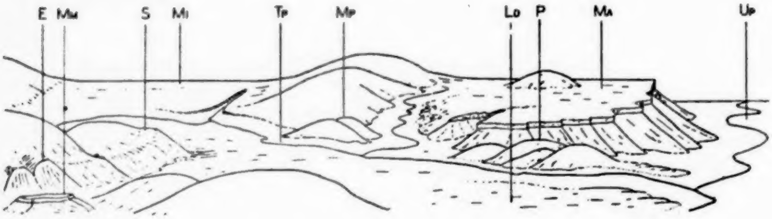
The marginal thinning of the deposits is entirely a function of the valleyward slope of the "Pedestal", or pre-alluvial surface. Beneath the axial terraces this surface appeared quite level, but two miles from the northern edge of the valley it was found to slope towards the river with a gradient of 1 in 50, while less than half a mile from the margin the terrace deposits were only 40 feet thick.

The Intermont Surface.—As mentioned above, there is no break of slope between the Main Terrace surface and its continuation among the hills to the north, to which the name "Intermont Surface" has been given (fig. 2). North-east of the section line L–M in fig. 2, this surface was found to be cut across the schists, and rose very gently northwards, although near the valley margin subsequent regrading had steepened the slope to as much as 1 degree. Steep-sided schist and dolomite hills rose with surprising abruptness to heights of 500–600 feet above this rock-cut surface (Plate XXVII*b*). On the other hand, where the Intermont Surface is being dissected by the right-bank tributaries of the Ugab shown in fig. 2 river terraces reveal up to 50 feet of deposits. Where the surface, as here, is depositional, the transverse gradients, like those of the Main Terrace, are negligible.

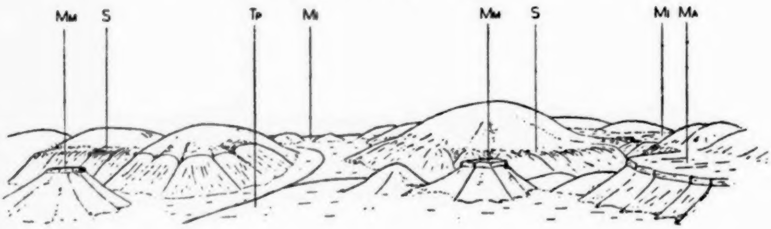
The distinction between Main Terrace and Intermont Surface is arbitrary and the two are genetically linked as well as physically contiguous (see fig. 6, A). One is taken as representing the infilling of the main valley, the second the partial burial of tributary plains and the lower slopes of adjoining hills. At the same time, in the latter region, the accumulating valley-fill would constitute a rising and eventually a stable base-level towards which gentle transport slopes would be developed across bare rock surfaces. Under these conditions the development of waning hill-slopes would be prevented, and the effect of shifting, episodic streams would be to extend the planed rock surface, sharply isolating the residual hills.

Rock Benches at the Main Terrace Level.—Bordering the Rotstein (Pt. B in fig. 2) there is developed a broad, level bench, while near it, and to the east, is a conspicuous flat-topped hill, presumably isolated by later erosion (Plate XXVII*b*). Both surfaces are cut into resistant quartz-porphyries. They are merely the first of numerous benches and flat-topped spurs seen to be developed downstream. The identity of level with that of the Main Terrace was unmistakable.

Two possible explanations of these features present themselves:



The relationship of the Main Terrace to the intermont surface North of the Ugab, and the measure of regrading achieved by tributary streams



View northwards from Main Terrace outlier, illustrating the relationship of shelf and intermont surface

Fig. 6 (A and B).

(i) That the rock-cut surface is earlier than the Main Terrace. It then could represent an earlier valley floor into which the pre-alluvial Ugab cut down, and which has survived through the superior resistance of the quartz-porphyry. One must then postulate that the subsequent valley-filling seen in the Main Terrace deposits reached this same level.

(ii) That the surface is contemporary with, or just younger than, the Main Terrace. At this period the Ugab could be imagined as flowing across ,the upper surface of the Main Terrace in a series of braiding channels, similar to its present bed. Below the Rotstein it is probable that the alluvial surface was much narrower, and that the stream would frequently transgress on to bare rock slopes, effecting the planation seen to-day.

The second view is held to be the more likely one, partly because, under it, there is no need to postulate a chance filling of the valley to a previous floor-level, partly because it explains the distribution and relative freshness of the feature. These benches and flat-topped valley spurs are therefore regarded as erosional equivalents of the Main Terrace.

Just as the Main Terrace proper is continuous with the depositional

portions of the Intermont Surface, so these rock benches must correspond to the erosional parts of the latter. The difference is merely one of extent and transverse slope. The benches are confined to a strip on the margins of the valley, at a point where a resistant rock bastion projects into it. They were therefore probably planed by lateral shifting of the main stream, thus explaining their striking flatness, and complete identity of level with the Main Terrace itself.

Summit-Planes at the Main Terrace Level.—Just across the river from the benches described above stands a group of flat-topped schist hills, whose dissected summit-plane is a direct continuation of the bench-level. The original hilltop surface is ascribed to the same agency as the benches, the greater degree of subsequent dissection being merely a function of rock-type. A second, similar group of hills, 5 miles N.N.W. from the first, and lying in an embayment within higher hills, may have a like origin, except that in all probability it represents a tributary planation, and may thus be regarded as a dissected outlier of the "erosional" Intermont Surface.

The Pedestal Surface.—The nature of this pre-alluvial surface has been described in connection with the overlying terrace deposits. After the destruction or undermining of the upper capping these deposits are fairly easily removed, and the former valley floor is laid bare as a marginal "shoulder", suggestive of a rock pedestal supporting the terrace proper. Below terrace sections the schists are seen to be deeply weathered, sometimes kaolinised, and often covered with a surface detritus, the whole having subsequently been permeated by lime-bearing solutions.

Complete removal of the overlying deposits produces characteristic flat-crested hills found near to the edge of the Main Terrace, to which their relationship can thus be observed. The exposed surface is usually cut by deep, narrow valleys working along strike and cleavage lines, and these directions control the form and pattern of the residual hills. In one case (near the section line J–K in fig. 2) the Pedestal Surface is preserved in a line of schist hills which are seen to pass north-westwards directly into the rock basement of the marginal terraces.

Because of this dissection the Pedestal Surface yields little quantitative information about the form of the pre-alluvial valley. The only slope measurements were obtained from the northern margins, as mentioned above. The evidence points to a broad, flat-floored valley whose southern limits are unknown, but which in the north abutted sharply against the bordering dolomite hills.

The Shelf.—Above the steep lower slopes of hills bordering the valley in the north, where the Main Terrace is absent, there is generally found a narrow shelf. This feature is particularly well developed around the valley embayment west of the section line E–F in fig. 2. Near the outlets of small

tributary valleys it widens—in one case to more than 200 yards across—and where this happens the surface becomes almost horizontal. More commonly it slopes outwards and at its inner edge grades smoothly into the hill-slopes above. These are everywhere gentler than those below the outer shelf edge. In more exposed positions, as for instance near Pt. L in fig. 2, it has been so eroded that it now appears only as a slight break in slope (the "Eroded Shelf" in fig. 2).

Plate XXVIII*b* shows its relationships to the marginal terrace. The Shelf was found on the same level as the surface of adjacent marginal terraces, and where it had a marked transverse slope an approximate continuation of that slope was to be seen in the Pedestal surface.

The suggested mode of origin is shown in fig. 7, the Shelf being regarded as part of the pre-alluvial valley-side slightly regraded to the surface of

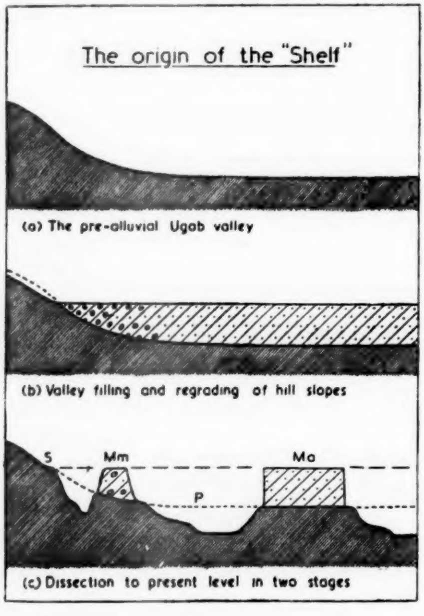


FIG. 7.

the later valley-fill. Where the valley-fill remains intact the form of hill-slopes above the Terrace is in accordance with this conclusion. In places the Shelf has retained a thin cover of coarse sandy conglomerates equivalent to the coarsest material found in the marginal terrace sections.

In contradistinction to the rock benches already described, the Shelf is developed in parts of the valley unlikely to have undergone planation by the main stream. Subaerial slope grading and lateral erosion by tributary streams emerging at the Shelf level are considered to be the causal processes. Occasionally the Shelf has an unexplained longitudinal slope, due to some form of tributary grading. Small valleys within the hills as well as larger outlets from the Intermont Surface beyond either are or were clearly graded to the Shelf. The latter forms a direct continuation of the erosional portion of the Intermont Surface, and as shown in fig. 2 is best developed where that surface borders the present valley, between the surrounding hills (fig. 6, B).

Subsequent erosion has in general followed the contact between limestone and schists. The resistance of the dolomites and the rapidity with which down-cutting has progressed in the schists are reflected in the steepness of the lower slopes and the depth and narrowness of tributary valleys cutting down through the Shelf. This rejuvenation has taken place in two stages which will be described below.

South of the river, the longer slope to the Ugab–Omaruru divide comprises an area of dissected schist hills, few of which rise above the terrace-level. The Ozongombe Hills (fig. 4) are typical of the larger features. Surrounding some of these hills a shelf, or high pediment, was observed, at a height comparable with that of the Main Terrace surface. On hills nearer the river the shelf becomes more extensive, leaving only a few summits rising above a general plateau level. Finally, it is continued in the flat summits of a group of schist hills close to the main stream. Assuming that the relationship of shelf to valley-fill is the same in the south as elsewhere, its development here, together with the Otjimakona terrace remnant, points to a former wide distribution of the Main Terrace south of the river.

2. *Lower Terraces.*

Incision of the valley below the Main Terrace level has taken place in two stages, the first of which produced a Lower Terrace 100–120 feet above the present river bed. Unlike the Main Terrace this is almost wholly an erosional feature.

(a) *Erosional Forms.*

(i) Long, gentle slopes, cut across Damara schists, grade smoothly upwards into the valley margins, or end more steeply against the Pedestal "shoulder" below the Main Terraces. At the outer edge the descent to the present river plain is abrupt, and there is no doubting the separateness

of the two cycles. The schists are generally weathered and calcified and often bear a capping of grey-white surface limestones up to 6 feet in thickness. Where this capping remains, terrace remnants appear as isolated ridges showing a slight but regular slope towards the present valleys. Over wide areas, particularly near tributary valleys, the terrace has been thoroughly eroded into numerous low hills, which may yield only traces of the former surface (the "Dissected Lower Slopes" of fig. 2).

(ii) A truly horizontal surface is developed near the Rotstein, where it is preserved in the long spurs whose flatness is strikingly apparent in Plate XXVIII*b*. Downstream it becomes more extensive, dominating the central parts of the valley. The spurs may extend unbroken into the adjoining hills or terminate abruptly against the higher rock benches already described. In form they closely resemble the latter though they are much more widespread. They may possess a surface limestone covering. Near the river the surface is lost in a maze of small, steep-sided hills.

The difference between these two erosional forms of the Lower Terrace would appear to be that between a planed valley floor in the latter case and gentle tributary slopes in the former. The occurrence of the level rock spurs adjacent to the similarly explained features of an earlier cycle supports this view.

(b) *Terrace Deposits.*

(i) Only in one area, traversed by the section line D–E in fig. 2, was any depth of alluvial material found on the Lower Terrace near the centre of the valley. Here, 20 feet of deposits were seen to overlie the schists. A basal sandy conglomerate was overlain by 6 feet of dark brown sands with a conglomeratic upper horizon. The section was topped by the same surface limestone which characterises most of the undissected Lower Terrace. The deposits lay between 80 and 100 feet above river-level. They were probably localised, and appeared to thin out, beneath the limestone cover, away from the river, but it must be noted that the Ugab here swings closely against the terrace edge, and that other sections less conveniently placed may have passed unnoticed. Their well-sorted character and the predominance of sands are suggestive of the axial facies of the Main Terrace, from which they may well be derived. These Lower Terrace sands and gravels are considered to be remnants of a minor depositional phase, probably restricted to the main channel.

(ii) Other Lower Terrace deposits, very dissimilar to the above, are confined to the valley margins and to tributary gorges. Both the areas marked in fig. 2 are found within, or at the debouchment of tributary valleys, and are associated with the first phase of the rejuvenation already mentioned.

Within the westernmost valley the most recent erosion cycle has progressed about 200 yards upstream. In this stretch the Lower Terrace is represented by narrow shoulders above a sheer rock gorge. The gorge ends at the nick-point, a series of steep drops in the stream bed where the shoulders referred to above pass into the undissected valley floor. This valley is itself sunk into an earlier, more open feature, graded to the marginal Shelf. On the valley shoulders below the nick-point and on the valley floor above are preserved the coarse, cemented breccias and conglomerates shown in Plate XXX*a*. The material is angular or sub-angular and little-sorted, and resembles most closely that found on the Shelf. It provides a clue to the origin of the marginal facies of the Main Terrace.

In the second case, similar deposits overlie a fan-shaped platform produced by lateral swinging of the tributary stream at its outlet into the main valley.

The Lower Terrace represents a considerable achievement in erosion, for not only were up to 300 feet of Main Terrace deposits removed over a wide area, but 100 to 150 feet of country rock was planed off within the valley. The small measure of regrading achieved by tributary streams in the hills to the north might be held to support the view that the time involved was not correspondingly lengthy. The hanging tributary valleys certainly indicate rapid erosion by a main stream more powerful than the local drainage. This is supported by the width of planed rock-slopes near the Rotstein. However, while it survived, the Main Terrace must have formed the base-level for these northern streams, and since it was excavated from the south, the period of tributary rejuvenation may only correspond to the later part of the cycle. South of the Ugab, tributary erosion has been much more effective.

There is evidence for only a short depositional phase following the Lower Terrace planation. This, in turn, was followed by surface limestone formation, covering the river deposits as well as the valley floor and slopes.

The Dissected Surface, South of the Ugab River.—The slopes towards the Ugab–Omaruru divide are of particular interest, partly since they provide a link between the river terraces and the erosion surfaces of the plateau, and also as a source of information about the earlier form of the southern margin of the Ugab Valley and the previous extent of the Main Terrace. Since they comprise 700 square miles of broken country, crossed by few tracks suitable for motor transport, with the added obstacle of wide, sandy river beds, no overall survey was possible. Traverses were made across the area, and information gained in this way, with the help of Hoffman's map of 1917–18 * and a contoured map of the Otjohorongo Native Reserve, formed the basis of the section in fig. 4. These are intended to show

* Accompanying the article by Maack (1923).

diagrammatically the height-relationships of the different surfaces rather than exact quantitative detail.

In contrast to the slopes north of the valley, where youthful tributaries break through the steep dolomite hills, these schist lowlands are traversed by broad tributary plains, following the regional slope north-westwards to the Ugab. At approximately right angles, along the Damara strike line, run the lines of prominent hills shown in fig. 4. At lower levels, between the rivers, a belt of quite sharply dissected country with low, flat-topped hills rises gently southwards. In the area studied it is limited to the south-west by the Otjongundu Plateau and the Okenjeje Complex; in the south-east it extends as far as Otjihorongo Mt.

Reuning (1937) recognised two erosion levels in this area, both below that of the "Kalkterrasse". The older was the hilltop surface extending across the low, rolling schist country, and which for convenience will be referred to as the "schist surface", the younger, that of the encroaching tributary plains.

Mention has been made above of an erosion surface corresponding to the Main Terrace and appearing either as a shelf surrounding higher hills such as the Ozongombe Hills at some distance from the Ugab, or as a complete or partial summit planation of hills nearer the main stream (Plate XXIX*a*). Valleywards from these hills the shelves descend gradually, as dissected pediments, to the "schist surface". To the south, however, broken higher ground persists, rising above the "schist surface" though not to any common level. South again, the lower slopes of Okenjeje Mountain and the Otjongundu Plateau end abruptly against the more recent planation levels, forming blunt-nosed spurs 400 to 500 feet above the corresponding Main Terrace level. It would seem that the adjacent groups of hills represent the unconsumed portions of a topography distinct from and older than the "schist surface", and which has locally been planed off at the shelf-level. The "schist surface" only becomes apparent as an unbroken planation product near the tributary valleys and towards the main stream. Followed northwards, it rises relative to the tributary plains and near the main flood-plain it is reduced to lines of low hills showing identity of level with the Lower Terrace (the "Dissected Surface" of fig. 2).

By projecting the Main Terrace level on to the section in fig. 4 it appears that the valley-fill must have feathered out 9 or 10 miles south of the main stream, although locally burying an irregular topography to greater depths.* Along its southern margins, the valley would show the same alternation of erosional and depositional surfaces, as does the Intermont

* The Otjimakona terrace fragment, for instance, occupies a former depression, and adjacent hills rise to slightly higher levels.

Surface to-day, in the north. The distribution of the circum-montane shelf indicates that at this time only a few areas rose above the valley-fill between its southern limits and the present line of the river. These were either trimmed marginally by tributaries or planed off by the main stream.

Removal of the uncemented valley-fill and the establishment of a tributary drainage would be a comparatively rapid process in the south, leading to the development of a widespread surface across the schists at the Lower Terrace stage. Later erosion has transformed this into the "Dissected Surface" mapped in fig. 2.

3. *Present Valley Plains.*

The Ugab plain, whose extent is shown in fig. 2, is a depositional feature, everywhere floored with a sandy, calcareous alluvium. In the east of our area it abuts directly against the Main Terrace and eventually widens to as much as 8 miles in the zone of terrace dissection. Against the Lower Terrace spurs in the west the flood-plain narrows, and below Oresuwa (fig. 4) almost disappears. Numerous residual features rise from within the plain, such as the terrace "mesas" or the limestone hills between Pts. L and N in fig. 2. The incised nature of the main valley near Pt. L may indicate a recent shift of course so typical of these braiding, seasonal rivers. The plain shows little transverse slope, and locally small tributary streams end in vleis without reaching the main channel.

The river has recently cut down, and now runs in a rock-floored bed between sandy banks 10–20 feet high. This erosion increases westwards, where the Ugab is occasionally seen cutting into solid rock. Dissection of the adjoining plain is being extended by gullies. This erosion is certainly being speeded by overstocking, consequent upon the development of karakul farming in the area, but it is doubtful whether its inception can be attributed to this cause, the valley only having been opened up in the last fifteen or twenty years.

The change in character of the present valley near the Rotstein is in accord with the evidence from the Main and Lower Terrace levels. This seems to be a critical point in the course of the river and corresponds to the passage from the Central Hereroland Plateau to the Transitional Plains, as defined in the introductory setting.

South of the Ugab, broad tributary plains lead smoothly to the plateau between the dissected surfaces already described. They provide an excellent illustration of the mechanism of river erosion in such regions. The sandy channels are repeatedly abandoned during successive periods of flow, producing wide, level surfaces from which incised tributary gullies eat back into the adjoining schist hills. Although the river-plains and winding

stream-courses convey an impression of "old age", the longitudinal gradients are of necessity steep. One such river was found to enter the main flood-plain with a gradient of 1 in 180—five times that of an equivalent perennial stream under a humid climate.

North of the main stream a few tributaries provide steep transitional slopes from the Intermont Surface to the present valley floor. An example of northern tributary drainage is reproduced from a field-sketch (fig. 6, A). Within the terrace-fill these streams are confined to narrow gorges, but across the schists they rapidly flare out into tributary plains between the confining limestone hills.

4. *Surfaces beyond the Valley Margins.*

(a) *The African (Inselberg) Surface.*—South of the Otjongundu–Otjihorongo line, the plateau rises with a convex slope, reaching the Ugab–Omaruru divide at heights of 3800–4100 feet. This plateau forms part of the "African" Surface, characterised by the completeness of its planation and by its residual inselberge. As an erosion surface it provides a useful datum line in comparative studies, since where it *does* show marked slope it is a result of warping, or subsequent erosion.

One has here to account for an alternation of mountain and plain in contrast to the hill and valley relief of the normal landscape (Cloos, 1931). The inselberge are mainly "härtlinge",* and the problem in general is not that of escarpment retreat but of surface planation of the surrounding, less resistant rocks. There is general agreement that the explanation of these planation processes is to be found in the rhythm of a tropical steppe or savanna climate and the peculiarities of the seasonal or episodic streams compared with the perennial drainage of humid areas.

The abrupt contrast in slope between hillside and plain is paralleled by the difference in the nature of their detrital cover. The former are often covered in coarse scree, the latter in sand and fine gravel. Only this finer material is being transported, and then only spasmodically, by the numerous shallow channels during their short "flood-life" following heavy rains. Because of the copious supply of fine material the streams are overloaded from birth, channel incision is prevented, and the braided pattern of shifting courses comes into being, dissipating the energy of run-off over a wide area and leading to the areal planation already described. The absence of a continuous vegetative cover allows free play to this process.

The break between mountain and plain is further emphasised by the relationship of the inselberge to the drainage pattern. They form neither

* Only the granite exfoliation domes would be termed "Bornhardts" in the sense used by King (1949 *a*).

the primary watersheds, which are usually determined by regional axes of warping, nor the secondary interfluves. This is the basis of the difference in detrital cover already mentioned. The rivers do not form the link between mountain and plain, and only the comminuted weathering products removed as hill-wash enter the drainage system. This independence of mountain and stream, aided by lateral planation at the foot of slopes, is reflected in the absence of the waning slope, which characterises the inselberg landscape.

Overall planation implies the prior development of graded regional slopes. The inselberg landscape is an old-age form as shown by its relationship to exposures of the Fundamental Complex. Where it now occurs at great heights above sea-level it indicates regional uplift or warping, for selective incision of drainage systems would be inimical to its development. Similarly, down-cutting by exogenetic through-going drainage, if accompanied by widespread tributary erosion, would modify the regional planation surface and lead to the development of concave, waning hill-slopes.

Many writers have stressed the fact that the climate now prevailing in this area can adequately explain the land-forms of the plateau, and that the evolution of this landscape is still in progress. However, an examination of hill-slopes enables one to differentiate between the areas north and south of the Otjongundu–Otjihorongo line. To the south the inselberg land-forms remain practically unmodified, but in the north the Ugab and its tributaries have eroded vertically as well as laterally, and this is shown by the appearance in the landscape of transitional waning slopes. The distinction can be usefully employed in delimiting the sphere of activity of the Ugab drainage in this area, and with it the remodelling of the "African" Surface.

(b) *The Franzfontein Summit Plane.*—Not less striking than the even skyline presented by the "African" Surface on the plateau south of the Ugab River, is the summit plane of the Franzfontein Mts. On hills within the valley, it stands between 1200 and 1300 metres above sea-level (3950 and 4265 feet). This is the approximate height of the Ugab–Omaruru divide. It rises northwards and eastwards across the dolomite ranges. Eastwards, the slope is 1 in 300, approximately that of the Ugab River in this area. Northwards, it rises with an initial gradient of 1 in 250 and appears gradually to flatten out. These gradients are commensurate with those observed on the plateau surface south of the river.

If the northward continuation of the "African" Surface lies in this summit plane, it demonstrates a mid-Tertiary transverse warping along the Otavi axis (du Toit, 1933), corresponding to the northern margin of the "shallow down-warped trough of the Khomas peneplain" referred to by Gevers (1936). The Intermont Surface must represent erosion of the weaker intervening schists from earliest Tertiary times onwards. South

of the river these schists have been almost completely dissected and the warped surface modified beyond recognition.*

(c) *The Pre-Karroo Surface.*—An examination was made of the pre-Karroo Surface in the Otjongundu Plateau to discover what part, if any, it played in the present landscape. The boundary between the Karroo and older rocks, with a section through the Plateau, is shown in fig. 4.

In the south-east, the sediments already described rest upon schists, the contact lying 150 feet above the base of the Plateau. In the north-west the pre-Karroo floor is everywhere formed of Salem granite and is very uneven, sometimes rising to 300 feet above the adjoining river-plain. The contact between granite and schist forms an approximate north-western limit to the Otjongundu Plateau. Measurements taken here showed the pre-Karroo Surface to be rising between 1 deg. 30 min. and 4 deg. towards the south-west, while from a barometric traverse along the south-west side of the Plateau the contact between schists and later sediments was found to rise gently in the opposite direction, as though the Karroo beds are resting on an asymmetrical ridge. The average height of the pre-Karroo Surface is 700 feet less than that of the "African" Surface on the Ugab–Omaruru divide.

The coarse nature of the sediments, not only here, but in the equivalent strata in the Erongo and Brandberg, supports the view that the pre-Karroo planation was not advanced. On the west side of the Otjongundu Plateau, Martin † has noted small hills of Salem granite projecting up into the sediments beneath the lava flows. This is in accord with evidence elsewhere, where the pre-Karroo and later surfaces have been compared (Maufe, 1935). The surface has, moreover, been known to have undergone considerably more warping than the African Surface, by which the present relief is dominated. Wherever they are in juxtaposition, the latter lies below the pre-Karroo Surface. Cloos (1931) describes the inselberg surface as lying 100 to 200 metres below the base of the Karroo sediments at the Brandberg. In view of the initial unevenness and subsequent deformation of the pre-Karroo Surface, any attempt to relate it to summit levels above the African Surface must be purely conjectural.

* It is of interest to note here the suggestion of drainage superposition made by Jaeger and Waibel (1921) to account for stream patterns across the Erongo Complex, south of the river. There is no evidence of the inselberg summit plane which they postulate as a possible "originating surface".

† Personal communication.

D. The Ages of the Surfaces, and the Evolution of the Valley.

Only in the most arbitrary fashion can one affix an age to a land surface representing erosion from Karroo times onwards and which in places is still being actively shaped. Following King and Dixey (King, 1949 *b*), we may regard its "initial" age as the time of its completion at the coast. Kaiser (1926) has dated the "African" Surface in the Southern Namib as pre-Middle Eocene. It is there overlain by the Pomona Beds, remnants of which occur in a beach deposit of that period, if not earlier. From Namaqualand there is evidence of the advanced dissection of an earlier "Kaap–Stormberg" surface having been achieved before the Upper Cretaceous (Rogers, 1915).

In the interior, the gently warped "African" Surface passes beneath the silicified beds underlying the Kalahari Limestones and Sands. By analogy with neighbouring areas, we may date some of these silicified fluviatile deposits as Mid-Tertiary (Dixey, 1941). In the area under study planation must have been complete by earliest Tertiary times. The climate during this period need have been no more humid than at present, as shown by current erosion processes on the plateau. The inselberg landscape, the prominence of limestones as relief builders and the feldspathic nature of terrestrial deposits on the surface all support this view. In the Otavi district the climate must have been sub-humid at least, since karst features were formed in the dolomites prior to the recent surface deposits.

In the Southern Namib, two periods of river activity (Lower Eocene and Lower Miocene) are recognised as evidence of regional rejuvenation associated with wetter conditions, but with the onset of extreme aridity the information from terrestrial deposits ceases. The Central and Northern Namib, on the other hand, have shared in the rainier Pleistocene periods common to most of the sub-continent, and offer a record of river activity following the end-Tertiary–Pleistocene climax in the continental uplift. Generally, the early Tertiary valleys cut into the "African" surface were open and flat, whereas later rejuvenation is shown in a narrower incision of the river valleys, within which the record of Pleistocene climatic oscillations may have been preserved.

In these areas the valley forms of the Atlantic drainage have been determined by the amount of uplift and character of marginal flexuring as shown by the height and trend of the Great Escarpment. In the Central Namib strong uplift near the coast eventually reversed the east-flowing Lower Tertiary drainage of the Naukluft Mts. (Martin and Korn, 1937) and brought into being the spectacular canyons of the Khan and Swakop Rivers. In the case of the Ugab Valley, as described above, not only has

uplift been less, but the zone of marginal tilting extends farthest inland. The tilting has not been uniform, as shown by the gradient of the plateau and the degree of river incision. That part of the Middle Ugab Valley described in this paper lies just inland from the zone of steepest tilting, which has been the scene of most active vertical erosion. In our area gentler rejuvenation has favoured the formation of a more open valley by the original (Lower Tertiary) stream, rising in the wettest area in South West Africa. This differentiation in valley form above and below the Rotstein has been aided by the greater extent of easily eroded Damara schists in the former area.

TABLE II.

Climate.	Morphogenesis.
Semi-arid	Vertical and lateral erosion by the main stream and its tributaries. Seasonal accumulation of sorted, rounded gravels along the margins of the main channel. Deep weathering of rock surfaces.
Semi-arid to normal-arid (present-day climate)	Equilibrium conditions with intermittent erosion. Finer materials from upstream successfully transported. Pebble spreads denote declining phases of activity by shifting main stream. Coarse, subangular deposits confined to valley margin near tributary outlets. Abundant lime-bearing subsurface water in channel deposits.
Normal-arid	Deposition of sandy material, with intercalated pebble-beds, in axial tract. Accumulation of coarser, subangular material in tributaries and on margins of main valley. Vegetation limited away from stream channels. Rubble on valley slopes.
Normal-arid to extreme-arid	Material deposited from upstream consists of sand with small scattered pebbles. This decreases relative to locally derived conglomeratic material. True fanglomerates along valley margins. Ground water dries out, causing calcification of sands and forming surface limestones.
Extreme-arid	Reworking of river sands by wind.

Table II shows the probable results of rainfall fluctuations in the Middle Ugab Valley, such as could be used in an analysis of the terrace deposits and related erosion forms.

On these assumptions, the history of the Middle Ugab Valley subsequent to the formation of the "African" surface has been reconstructed as follows:

STAGES IN THE EVOLUTION OF THE VALLEY.	CLIMATE.
(*a*) Dissection of the "African" Surface and erosion of the pre-alluvial Ugab Valley, forming the Pedestal Surface. Deep weathering of schists.	Sub-humid to semi-arid.
(*b*) Rapid deposition of sandy material within the central part of the valley. Drying out of sub-surface moisture, and calcification of the sands and underlying weathered surfaces, with the formation of surface limestones on exposed rock-slopes.	Normal-arid to extreme-arid.
(*c*) Reworking of channel deposits by the wind, giving unstratified red sands of terrace sections.	Extreme-arid.
(*d*) Deposition of sands and intercalated gravel spreads on the earlier axial deposits and over the eroded surface limestones of the lower valley slopes. North of the valley, tributary erosion yields conglomeratic material. Vegetation within the shifting channels gives rise to rootlet horizons, associated with pebble beds.	Extreme-arid to normal-arid.
(*e*) Less material from upstream proportional to the locally derived conglomerates. Fanglomerates along the valley margins indicate ephemeral stream erosion, while the appearance of coarser conglomerates within the axial sections indicates the maximum phase of tributary erosion. The erosion of the higher rock benches and summit planes near Rotstein and the erosion and deposition forming the Intermont Surface ensue. Regrading of the valley sides and planation by main and tributary streams form the Shelf. The valley-fill, itself rich in lime, is permeated by lime-bearing solutions.	Normal-arid.
(*f*) Rapid drying out leads to calcification in depth of the sands and sandy conglomerates and the formation of the thick limestone terrace capping.*	Normal-arid to extreme-arid.
(*g*) Erosion to the Lower Terrace level and extensive regrading of the southern valley slopes, where removal of the less indurated valley-fill favoured an early resumption of tributary activity. Erosion of wide rock-spurs where the river impinges against the Rotstein.	Semi-arid.
(*h*) Deposition of reworked Main Terrace material along the axial tract, with coarser conglomerates and fanglomerates in and near the rejuvenated tributaries in the north.	Normal-arid.
(*i*) Formation of the limestone capping of the Lower Terrace.	Normal-arid to extreme-arid.

* The gradual increase in the importance of locally derived materials shown in the Main Terrace sections may have been a result of surface limestone formation along the watershed during the first arid sub-stage, with a resultant decrease in surface run-off during the latter part of the depositional cycle. The first stage of deposition may have been a very rapid one judging by the paucity of local material. Most of the "Marginal Terrace" accumulation falls within the second stage.

(*j*) The river continues to erode its bed to its present level, and removes nearly all trace of the preceding depositional phase in the centre of the valley. The southern slopes of the valley are further dissected (the Dissected Surface). Second phase of tributary rejuvenation in the north.	Normal-arid to semi-arid.
(*k*) Deposition of 15 to 20 feet of sandy calcareous alluvium in the main valley.	Normal-arid.
(*l*) Slight erosion of the unconsolidated river-plain deposits ensues. Seasonal planation and incision by tributary streams continues.	Normal-arid to semi-arid.

Direct evidence for the age of the pedestal surface and the Main Terrace deposits is lacking. The kaolinisation of the schists beneath the alluvial deposits suggests that the surface be equated with the similarly weathered peneplain of the Southern Namib which is covered by the pre-Middle Eocene Pomona Quartzites (Kaiser, 1926). In this case, the pre-alluvial Ugab would be of comparable age to the Upper Henkries Valley (Rogers, 1915), and the earliest Tertiary arid period evidenced both in Namaqualand and the Southern Namib would be that during which the Main Terrace deposits began to accumulate. In the Ugab Valley the depositional cycle falls into two stages, but there is no evidence to suggest that these represent the two separate phases of Tertiary river activity described from the Southern Namib.

The modification of the "African" Surface by the Ugab and its tributaries may thus have originated in a Lower Eocene period of river activity. The incision of the river and kaolinisation of the schists beneath the Main Terrace deposits show a climate more humid than to-day.* The valley floor (Trogfläche) traversing the Ugabschiefergebirge described by Cloos (1931) is tentatively ascribed to the same erosion period, since it is lowered below a summit plane which continues the "African" Surface on either side of the valley. Near the Brandberg the survival intact of an inselberg surface to the very edge of the river implies that tributary activity was less and that the climate was drier than in the area upstream.

The limestone capping of the Main Terrace is a feature of older terraces throughout South West Africa. Here it forms a direct continuation of the surface limestones of the Otavi district and is the equivalent, at least in part, of the Kalahari Limestone. The continuity of this limestone cover over quite sharp breaks in slope as well as its generally unfossiliferous state led Korn and Martin (1937) to regard it not as a sediment, but as a surface and sub-soil deposit, formed by the drying out of lime-bearing ground-

* In reconstructing past climates from events within the Ugab Valley it should be remembered that the surface limestones of the Otavi area, being continuous with the Main Terrace capping, were not yet in existence, and that run-off would be much higher.

a

The Main Terrace burying "pre-alluvial" relief north of the valley. Note the Franzfontein summit plane.

b

Higher rock benches and similar Lower Terrace features near the Rotstein.

a

Steep-sided hills rising abruptly above the erosional Intermont Surface.

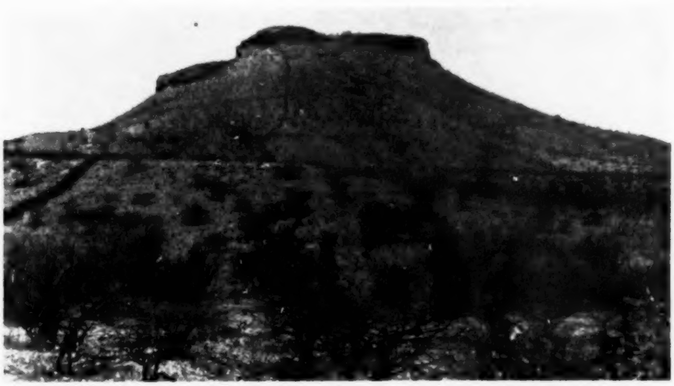
b

A tributary valley graded to the "Shelf" with a marginal terrace (Main Terrace) in the right foreground.

J. A. Mabbutt. *Neill & Co., Ltd.*

a

A partial summit plane at the Main Terrace level south of the Ugab.



b

The Pedestal Surface appears in the marginal shoulders of the "Sentinel", a Main Terrace fragment just south of the Ugab. In the foreground is the limestone-capped Lower Terrace.

a

Fanglomerate in a tributary valley north of the Ugab.

b

The African Surface with characteristic inselberg relief on the Ugab–Omaruru divide.

water, with the rapid onset of arid conditions. "The thickness of the limestone at any place is a function of its former saturation" (author's translation). It would seem to mark the end of a Tertiary wet phase in South West Africa.

The Main Terrace deposits may indicate the river erosion along the western margins of the Kalahari Basin, which ultimately provided the raw materials for the Kalahari Sand invasions to the north and east. Wagner (1910) has suggested that erosion of the Nosib Beds of the Otavi Series could have supplied part of these sands, and the Etjo Sandstones could be named as another possible source. The formation of surface limestones over the intervening area at some time during the Tertiary period seems to have sealed off the Ugab Valley from further deposits.

The most important feature of the succeeding erosion cycle is the sharp rejuvenation indicated by incision of the Ugab canyon below the valley floor described above. Above the shoulders of the Khan and Swakop canyons Gevers (1936) has noted deposits which are possibly equivalent to those of the Ugab Main Terrace. Should the suggested age for the Main Terrace be correct, the main climax of uplift and rejuvenation must date from the end of the Tertiary period.

From the Omaruru River near Erongo Mt. Cloos (1919) describes the dissection of a valley-fill comparable with the Main Terrace in the Ugab. Like the latter it consists of sands and pebble seams, with a surface limestone capping continuous with that on the adjoining "African" surface Unlike the Ugab, however, the Omaruru River has not yet cut down to its pre-alluvial floor. The differences are no doubt to be explained by differences in the amounts and consequences of rejuvenation and in the climate and extent of the catchment areas.

I am indebted to Dr. H. Martin for the following information concerning African Chelles-Acheul (Stellenbosch III–V) tools found in a "lower calcareous terrace" above the Uis River, at the east foot of the Brandberg. "The terrace in which the tools occur at the Uis River is cut into the calcreted fanglomerates surrounding the Brandberg, which are the equivalent of the Ugab Main Terrace. They slope from the Brandberg down towards the Main Terrace. The height of the Stellenbosch terrace is approximately 100 feet above the Ugab."

Although erosion of the Main Terrace obviously corresponds in part to the major Lower Pleistocene wet phase seen in the Vaal and Zambesi, the final stages of the cycle, as shown by the Uis River terrace, must be dated Middle Pleistocene, comparable with the Older Gravels at the Victoria Falls (Clark, 1950) or the Younger Vaal Gravels (Söhnge and Visser, 1937). No Lower Pleistocene deposits have as yet been identified, but the Lower Terrace may be of composite origin and represent two periods of increased

river activity corresponding to Lower and Middle Pleistocene wet phases.*

Within the unconsolidated materials of the valley floor, now undergoing dissection into a lowermost terrace, Middle Stone Age tools have been found.† The erosion below the broad flat floor of the Lower Terrace stage thus corresponds to an Upper Pleistocene wet phase, and the sandy calcareous alluvium is equivalent to the Younger Gravels of the Victoria Falls (Clark, 1950), and the grits, sands, and clay deposits of the Third Wet Phase in the Vaal River (Söhnge and Visser, 1937). The erosion of the alluvium may indicate a recent change to slightly wetter conditions.

The stages in the evolution of the Middle Ugab Valley, already described, can now be dated. Stage (*a*) represents a period of erosion dating from earliest Tertiary times. Stages (*b*) to (*f*), comprising the remainder of the "Main Terrace cycle", fall into the Tertiary period. The "Lower Terrace cycle" (stages (*g*) to (*i*)) is Lower and Middle Pleistocene, and the final, "Floodplain cycle" (stages (*j*) to (*k*)) is in all probability Upper Pleistocene, while stage (*l*) brings us up to the present.

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The isohyets in fig. 1, A are based on the map by the Meteorological Office, Windhoek, while the geological map is drawn from Reuning's map of Central South West Africa and the Omaruru Sheet of the Geological Survey.

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* I am grateful to the South West Africa Co. and to Dr. J. W. Brandt for information concerning the existence within the Lower Ugab Valley of "post-Tertiary river terraces of approximately three different levels lying several hundred feet below the Tertiary plain and formed in close association with the river channels as the result of recent continental uplift or drop in sea-level. Three terraced eminences have been noticed at the coast as well".

† Personal communication from Dr. H. Martin.

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THE ECOLOGY OF SOUTH AFRICAN ESTUARIES.

PART III. KNYSNA: A CLEAR OPEN ESTUARY.

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(With Plate XXXI and four Text-figures.)

(Read March 21, 1951.)

CONTENTS.

INTRODUCTION.

Part I of this series of papers outlined the conditions of life in estuaries. It was largely a review of work done elsewhere and it was intended as a basis for further studies of South African conditions. Part II described the Klein River Lake, one of the many estuaries in South Africa which are open for only part of the year. This paper, Part III of the series, describes the ecology of Knysna estuary. We started the work in 1947, but since then we have visited over thirty different estuaries along the South African coast-line so we now have a fair idea of Knysna's peculiarities. We can say at once that it has the richest fauna we have seen. We ascribe this

richness to the deep rocky mouth and the clarity of the water. These points are discussed in greater detail below.

Not only is the estuary rich in individuals, it is also rich in species. There are obvious changes in physical factors along the length of the estuary, and the faunistic changes are equally marked. Knysna is thus a good testing ground for the theories of distribution put forward so tentatively in Part I, and we have therefore concentrated attention on the physical conditions and the distribution of the fauna. In doing so we have limited the discussion to *common benthonic animals.* At the same time we have recorded in an Appendix all the animals we have collected except the fishes and the plankton.

We have omitted a list of the fishes because our own collections are very incomplete, and Professor J. L. B. Smith, who has studied the ichthyofauna of Knysna for many years, has a very large number of records. He has also seen our collections, and we hope that he will discuss the Knysna fishes in a separate paper.

Similarly, any serious discussion of the estuarine plankton demands not only more extensive collections than we have made; it also demands a knowledge of local marine plankton. The South African plankton has never been monographed, and we cannot get our estuarine samples identified.

None the less, we have listed in the Appendix a total of 357 species of animals. The great majority of these are new records for the area, which has never been systematically studied before. Some of them are new records for South Africa and there are quite a number of new species. This systematic work will form the subject of separate papers by ourselves or by the many authorities who are helping to identify our estuarine collections. In some cases we have not received their identifications at the time of publication of this paper. We have had to decide whether to omit these records altogether or to include them without specific names. We have decided on the latter course and have included the specimen reference number so that later, when the systematic papers are published, it will be possible to give each record a specific name.

The list of species in the Appendix is given in tabular form showing the stations where each species was collected. Symbols indicate the comparative abundance, habitat, and faunistic group to which each species belongs, if this is known.

Methods.

We have visited Knysna several times. The main collections were made by parties of biologists in July 1947 and November of the same year.

Since then we have returned at intervals, partly to check doubtful records and to collect further specimens at new stations, but mainly to get more data on the seasonal and yearly changes in temperature and salinity. In this connection we would like to record our appreciation of the help we have received from many friends and particularly from Messrs. Thesen & Co. and from Mr. van Dort, who has kindly allowed us to quote from his records of daily temperatures at Paarden Island.

Our gear has not been elaborate, and at this stage we have not attempted quantitative work. Most of the collecting was done by hand or with a spade and a sieve. We used a small 30-yard seine for catching small fish, a medium plankton net, a small dredge below tide marks, and a D net for shrimps and similar forms. This D net is a most useful piece of equipment. It is a conical bag of 1-mm. grit gauze about 10 feet long and 3 feet wide and is attached to a D-shaped frame which has runners on the straight side of the D. These serve to keep the frame upright and to prevent it digging into soft mud. It may be dragged by hand in the shallows or towed from a small boat in deeper water.

Salinities were determined by the Knudsen method, but no great accuracy is claimed for the results, which were titrated to two decimal places and recorded to one. It was felt that in an estuary where the salinity varies so greatly with the state of the tide, the daily rainfall, and the exact locality, laborious refinements were unnecessary. Temperatures were recorded with a centigrade thermometer calibrated to 0·5° C. immersed up to the reading level, and are probably accurate to 0·2° C. Unfortunately, no estimations of nitrate, phosphate, oxygen concentration, or excess base were possible with the limited equipment we used in the field. Measurements of pH were taken with a Lovibond comparator using standard discs and have an accuracy of 0·2.

Topography.

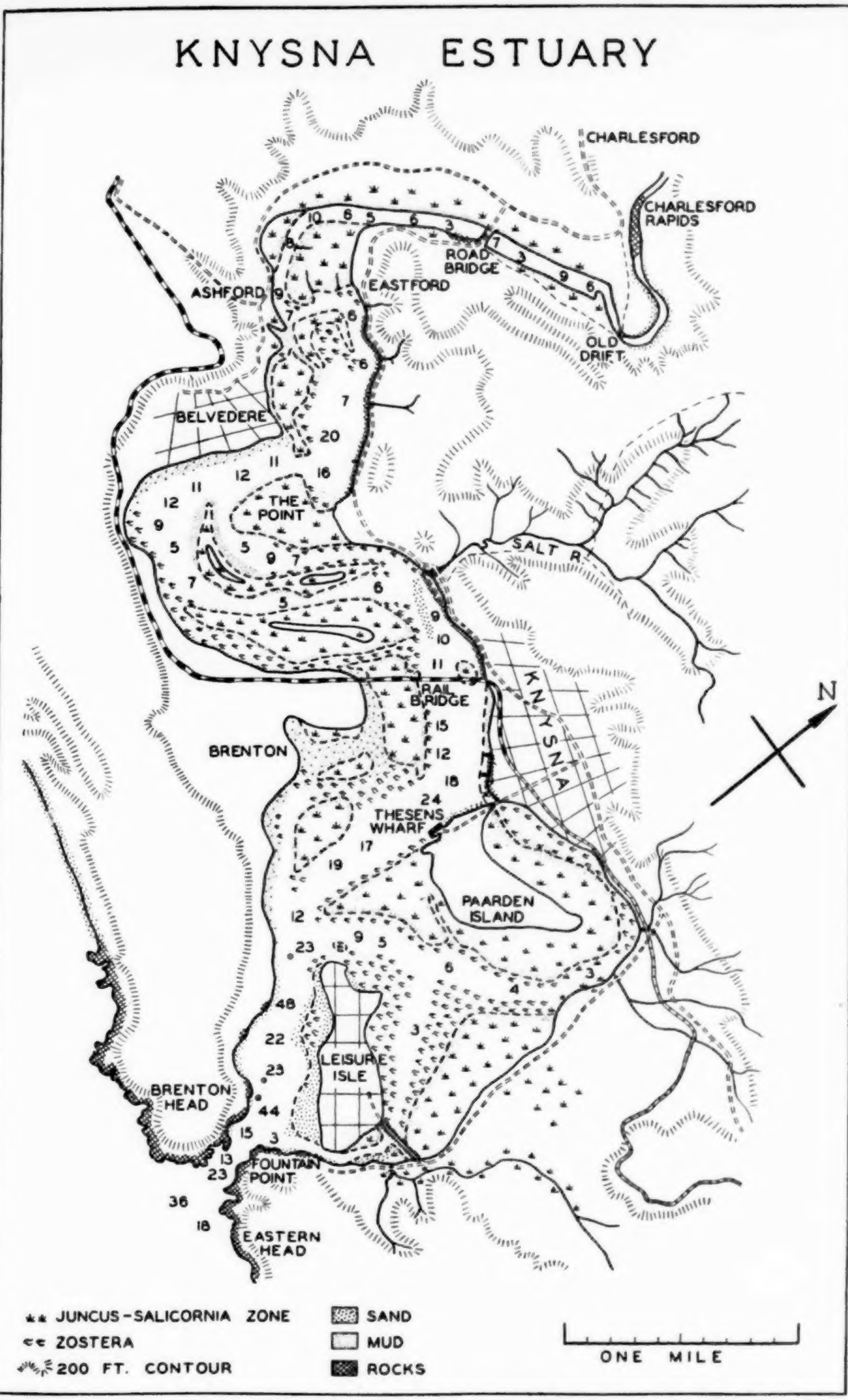
Between Mossel Bay and Port Elizabeth there is a well-watered coastal belt cut off from the dry uplands of the Union by the Outeniqua range of mountains. It is fifteen to twenty miles wide and two to three hundred feet high, but intersected at intervals by deep, forest-clad ravines formed by rivers which arise in the Outeniquas and flow over a series of rapids to the sea. The Knysna river is one of these. It is fifty miles east of Mossel Bay and one hundred and fifty miles from Port Elizabeth. It has a small drainage basin of about two hundred and fifty square miles, its length is about forty miles, and it is tidal for the last twelve miles. Along this tidal stretch the valley gradually broadens to form a wide lagoon, but at the sea exit there is an abrupt constriction where the estuary channel passes

between two massive headlands into the sea. (See aerial photograph, Plate XXXI.) The position of the mouth is 34° 4′ S./23° 3′ E.

Apparently the South African coast has been subjected to many vertical movements in past geological times. Thus Krige (1927) states that the Knysna and many other South African rivers "are true drowned valleys more or less silted up". One of the many pieces of evidence on which this statement is based is that "the maximum depth of the Knysna lagoon is 40 feet whereas recent borings for the new railway bridge have failed to find bedrock at 80 feet". It may be added that, since the completion of this rail bridge, the silting in the upper reaches has been accelerated. The depths of the upper channels are less than those marked on the admiralty chart drawn in 1924 and the mud banks are more extensive.

As shown by the sketch map (text-fig. 1), Knysna Estuary is an **S**-shaped stretch of water with a channel about twelve miles long. At Charlesford farm there is a series of shallow stony rapids and sandy pools between bushy banks. This stretch will be referred to as the Charlesford Rapids. Lower down there was once a stony ford or drift. This has long since been abandoned and is now known as the Old Drift. From here on, the estuary winds sluggishly between marshy banks past Westford Road Bridge to Eastford. Here the estuary widens and is beset by tidal banks of sandy mud overgrown with eel grass (*Zostera*), rice grass (*Puccinella*), and the small rush (*Juncus*) at different levels. It flows past Belvedere, The Point and Salt River, and under the Rail Bridge, becoming wider all the while. Below the rail bridge it is over two miles wide. The main channel here is twenty to thirty feet deep, but there are extensive tidal *Zostera* beds fringing the banks and also two permanent islands. The upper one is Paarden Island which is connected to Knysna township by a road from Thesen's Wharf crossing a narrow side-channel. Most of this island is boggy and covered with brack grasses. The lower island is Leisure Isle, a bush-covered sandy island used as a pleasure resort and connected to the east bank by a long narrow causeway over boggy salt marshes.

Below Leisure Isle the lagoon narrows and the channel reaches a maximum depth of fifty-one feet. At the same time the banks become progressively more and more rocky. At first there are only a few rocks projecting through the sand, then small reefs appear, and finally, when Fountain Point (also known as the Navigation Beacon) is reached, the whole shore is a tumbled mass of crags and boulders becoming more and more precipitous as one passes out between the Heads. Along this stretch one begins to feel the strength of the ocean rollers, and the crags on the shore beyond the Heads are pounded by surf and drenched by spray. In anything except calm weather the surf breaks on the bar, which is charted as thirteen feet deep.



TEXT-FIG. 1.—Sketch map of Knysna Estuary. The low-tide level is shown by broken lines and the high-tide level by unbroken lines. Drawn from the Government Trigonometrical Survey map and corrected from observations. Depths in feet from Admiralty Chart (corrected 1938).

Climate.

Knysna, like the rest of the Tsitsikama forest belt, has a warm climate and a good rainfall. The records for the period 1946–1949, when most of our work was done, are given in Table I below. The figures are average rainfalls in inches for six stations in the drainage basin, namely, Millwood, Sourflats, Belvedere, Gouna, Deepwalls, and Concordia. The averages for the fourteen years 1936–49 are also shown for comparison.

Table I.—Monthly Average Rainfall in Inches at Six Stations in the Knysna Drainage Basin.

Period.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Total.
1946 .	3·02	2·63	5·79	1·94	0·83	1·72	2·84	1·67	3·06	2·34	1·48	2·67	29·99
1947 .	2·86	1·90	4·26	2·97	3·15	2·52	5·53	0·73	3·74	2·59	2·62	2·10	34·97
1948 .	4·94	2·57	2·24	4·53	0·65	1·32	1·90	1·41	3·61	4·93	2·27	3·36	33·73
1949 .	4·47	3·02	0·72	2·97	3·94	0·23	1·10	1·97	3·33	2·47	5·99	1·75	31·96
Average 1946–1949	3·82	2·53	3·25	3·10	2·14	1·45	2·84	1·45	3·44	3·08	3·09	2·47	32·66
Average 1936–1949	3·39	3·18	3·32	2·42	2·74	2·07	2·74	2·20	3·98	3·41	3·64	3·21	36·30

An analysis of these figures shows the following points:

1. The maximum rainfall is in the spring and the minimum is in winter. Thus the three-monthly averages for the period 1936–49 are as follows:—

D.	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.
3·21	3·39	3·18	3·32	2·42	2·74	2·07	2·74	2·20	3·98	3·41	3·64
Average 3·26			Average 2·83			Average 2·34			Average 3·68		
Summer			Autumn			Winter			Spring		

It will be noted, however, that there is not really much difference from one season to another, and one would not expect large seasonal changes in salinity due to rain alone.

2. In all the four years we have worked on the estuary the rainfall has been below the fourteen-year average of 36·30 inches. It was highest in 1947 and lowest in 1946. We can thus expect higher salinities in 1946 and lower ones in 1947. This point will be discussed again later.

3. In certain months the rainfall was very different from that expected on the basis of the fourteen-years records. Thus the winter averages for

1946, 1947, 1948 and 1949 are 2·08, 2·93, 1·54, and 1·10 inches respectively, as compared with the fourteen-year winter average of 2·34 inches. It will be remembered that the river is short and the drainage basin small, so that excessive rain or an unseasonal drought is immediately reflected by salinity changes at the top of the estuary. This point also will be discussed later.

Since air conditions affect the rate of evaporation from the estuary and thus the salinity, these are briefly summarised here. The average daily temperature for the period 1932–40 is 16·8° C. varying from 13·0° in July to 20·8° in February. The absolute maximum is 33·5° C. recorded in January 1934, and the absolute minimum is 1·0° C. for July 1932. The average wind velocity at George for the three winter months is 2·6 metres per second, and 2·5 metres per second in the summer months. The relative humidity is 72 per cent. in the winter months and 80·8 per cent. in the three summer months. All the above data were obtained from the South African Meteorological reports.

The Physical Conditions in the Estuary.

Water Movements.—As shown in Part I of this series of papers, water movements have important effects on the substratum, the turbidity, and the salinity of estuarine waters. They are due to the flow of the river, to tidal currents, to waves coming in from the sea or stirred up by the wind. In all probability the absolute and relative strengths of these agencies determine the type of estuary that is formed.

In Knysna the river flow is seldom strong. The river is short and the catchment area small. The flow has no great effect below the Charlesford Rapids, but it is strong enough to maintain a well-marked salinity gradient from the Rapids to the sea. Once in ten or twelve years the river is said to come down in flood, staining the whole estuary brown and killing off much of the benthonic population. This phenomenon has not been observed.

The tidal rise and fall at the mouth at Springs is about six feet, and the mouth is sufficiently wide and deep to allow this tidal range to be maintained right up to Westford Bridge, where a maximum range of 6 feet 4 inches was recorded on 13/4/49. At the Old Drift, a mile farther upstream, the range had fallen to 5 feet 7 inches, but above this there is a steep rise over a series of rapids, and at Charlesford the tidal rise was only one foot. The delay in the low tide from the mouth to the Old Drift is approximately two hours at spring-tide. The delay in the high tide is very much less. This means that, as usual, the ebb-tide is of considerably longer duration than the flow.

The tidal movements up and down the estuary cause slight currents in

the upper reaches round Westford Bridge, well-marked ones at Thesen's Wharf, and dangerous ones in the narrow channel between the Heads. As usual, the strongest currents are in the main channels, which are deflected towards the bank on the outside of the bends. This is shown quite clearly in the soundings given in text-fig. 1, and was also evident from the varying grade of substratum at different points.

Wave action is terrific on the rocky shores at the mouth, but as one passes in between the Heads the seas rapidly diminish, and at Fountain Point the swells are very gentle. Farther upstream, where the estuary widens into a lagoon, they disappear entirely. On the other hand, this broad stretch of water is easily affected by winds blowing up and down the river. The waves so formed rapidly stir up the soft mud in the shallows but have no obvious effect on the fauna.

Salinity and Temperature.—Records are given in Table II. All these records are from surface samples. A comparison of surface and bottom samples at the mouth showed no vertical salinity gradient, and it is suggested that the churning on the bar, together with the irregularities of the channel prevent vertical layering in this region. A record taken at Westford road bridge on 10/7/50, however, showed a salinity of 4·4°/₀₀ at the surface and 30·0°/₀₀ at the bottom (depth of 8 ft.). This record was taken at high tide just after the turn and shows distinct layering, with the fresh river-water flowing downwards over the surface. Unfortunately, the vertical salinity gradient in this region was only appreciated towards the end of the survey and we are thus unable to say how far it extends, and whether it is entirely restricted to the upper reaches of the estuary. This point is stressed because Yonge (1949) and previous authors have remarked on the importance of vertical salinity gradients on the distribution of the biota.

The records of salinities and temperatures are by no means as complete as we would wish. Knysna is over three hundred miles from our Cape Town base, and only records taken at high and low tide are of any value. For this reason odd records had to be taken whenever opportunity permitted in the midst of other work. None the less, the records taken illustrate several important points.

A. *Seasonal Differences.*—A comparison of summer and winter temperatures shows that the maximum and minimum temperatures are recorded at the top of the estuary and vary from 12° C. in winter to 29° C. in summer. Exceptions to this statement are due to the fact that occasionally very low temperatures (*e.g.* 11° C.) are recorded at the mouth in summer. This is due to a cold sea current, which will be discussed later and does not alter the general statement that the maximum seasonal variations occur at the top of the estuary. It will also be noticed that the estuary is warmer than the

TABLE II.—THE PHYSICAL CONDITIONS IN KNYSNA ESTUARY.

Station and Distance from the Sea.	Date.	Temperature °C.		Salinity ‰		Tidal Range (ft.).	pH.
		High Tide.	Low Tide.	High Tide.	Low Tide.		
Fountain Point (0·4 miles)	10/7/46	15·0	13·9	35·4	35·1		
	10/7/47	..	14·7	..	31·3		
	31/5/48	17·1	16·0	..	..		
	9/7/50	..	15·3	..	34·2		
	14/7/50	..	..	36·7	..		
	Winter Av.	15·3		36·1	33·5		
	15/1/46	21·8	..	35·4	..		
	26/11/47	..	..	35·0	33·7		
	2/3/48	11·5*	16·2*	..	..		
	3/3/48	..	16·2*	..	..		
	22/12/48	..	22·2	..	35·1		
	13/4/49	..	..	35·8	35·7	6′ 3″	8·3 (low) 8·4 (high)
	14/4/49	19·0	20·0	..	..		
	5/1/50	11·0*	16·6*	36·0	36·3		
	Summer Av. without cold current	20·8		35·6	35·2		
	Yearly Av. Salinity			35·7	34·5		
Thesen's Wharf (2·6 miles)	12/7/46	16·2	12·9	35·0	33·2		
	12/7/47	..	..	..	23·9		
	10/7/50	16·0	..	32·0	..		
	12/7/50	..	14·3	..	29·9		
	Winter Av.	14·9		33·5	29·0		
	14/1/46	22·2	..	35·3	..		
	13/4/49	..	..	35·7	35·1	6′ 5″	8·5 (low) 8·5 (high)
	14/4/49	19·5	20·0	..	..		
	5/1/50	11·5*	24·0	36·1	35·2		
	Summer Av. without cold current	21·4		35·7	35·2		
	Yearly Av. Salinity			34·8	31·5		
Rail Bridge (3·4 miles)	11/7/46	16·2	..	35·2	..		
	17/7/47	14·0	..	32·0	..		
	31/5/48	14·9	14·2	..	..		
	9/7/50	12·0	..	22·6	..		
	12/7/50	..	14·3	..	29·1		
	Winter Av.	14·3		29·9	29·1		
	8/1/46	..	24·2	..	33·5		
	2/3/48	17·4*	21·3	..	..		
	3/3/48	..	22·2	..	..		
	Summer Av. without cold current	22·6		..	33·5		
	Yearly Av. Salinity			29·9	31·3		

* Cold current.

TABLE II.—THE PHYSICAL CONDITIONS IN KNYSNA ESTUARY.—*Contd.*

Station and Distance from the Sea.	Date.	Temperature °C.		Salinity ‰		Tidal Range (ft.).	pH.
		High Tide.	Low Tide.	High Tide.	Low Tide.		
The Point (6·1 miles)	11/7/46	14·2	. .	34·6	. .		
	17/7/47	13·5	. .	31·6	21·7		
	31/5/48	16·7	15·1	. .	. .		
	10/7/50	18·0	. .	29·1	. .		
	12/7/50	. .	15·0	. .	28·7		
	Winter Av.	15·4		31·8	25·2		
	11/1/46	23·2	. .	34·6	. .		
	2/3/48	22·0	23·5	. .	. .		
	3/3/48	. .	22·7	. .	. .		
	14/4/49	19·5	20·5	. .	. .		
	5/1/50	17·0*	24·1	35·9	34·9		
	Summer Av. without cold current	22·1		35·3	34·9		
	Yearly Av. Salinity			33·2	28·4		
Westford Bridge (9·7 miles)	12/7/46	15·4	12·2	28·6	24·1		
	20/7/47	13·0	12·0	14·8†	5·4†		
	31/5/48	17·5	16·0	. .	. .		
	10/7/50	15·6	. .	4·4‡	. .		
	12/7/50	. .	13·0	. .	12·2		
	Winter Av.	14·3		15·9	13·9		
	28/11/47	. .	. .	. .	. .		8·2 (low)
	2/3/48	22·5	25·9	. .	. .		
	3/3/48	. .	25·2	. .	. .		
	21/12/48	. .	21·2	. .	4·5		
	24/12/48	23·8	. .	17·2	. .		
	13/4/49	. .	. .	33·5	27·7	6′ 4″	8·1 (low) 8·2 (high)
	14/4/49	21·0	22·0	. .	. .		
	5/1/50	27·0	27·0	31·9	24·9		
	Summer Av.	24·0		27·5	19·0		
	Yearly Av. Salinity			21·7	16·5		
Old Drift (10·7 miles)	22/7/47	. .	12·0	. .	1·4†		
	31/5/48	17·3	14·6	. .	. .		
	10/7/50	14·0	. .	1·3‡	. .		
	12/7/50	. .	13·5	. .	5·1		
	Winter Av.	14·3		1·3	3·3		
	28/11/47	. .	. .	7·4	. .		7·2 (low)
	2/3/48	23·2	26·7	. .	. .		
	3/3/48	. .	25·7	. .	. .		
	21/12/48	. .	21·0	. .	1·1		
	24/12/48	22·5	. .	2·9	. .		
	13/4/49	. .	. .	28·9§	17·6§	5′ 7″	7·3 (low) 8·0 (high)
	14/4/49	22·5	21·5	. .	. .		
	5/1/50	29·0	27·5	26·9	18·6		7·6 (low)
	Summer Av.	24·4		16·5	12·4		
	Yearly Av. Salinity			13·5	8·8		

* Cold current. † Rain. ‡ After rain. § Drought.

TABLE II.—THE PHYSICAL CONDITIONS IN KNYSNA ESTUARY.—*Contd.*

Station and Distance from the Sea.	Date.	Temperature °C. High Tide.	Temperature °C. Low Tide.	Salinity $^{\circ}/_{\circ\circ}$ High Tide.	Salinity $^{\circ}/_{\circ\circ}$ Low Tide.	Tidal Range (ft.).	pH.
Charlesford Rapids (11·8 miles)	10/7/50	13·0	..	0·3	..		
	12/7/50	..	12·2	..	0·4		
	Winter Av.	12·6		0·3	0·4		
	28/11/47	..	..	..	2·5		7·0 (low)
	15/4/49	..	..	20·4*	11·2*	1' 0"	7·0 (low) 7·5 (high)
	5/1/50	28·0	27·3	0·9	1·5		6·6 (low) 6·8 (high)
	Summer Av.	27·7		10·7	5·1		
	Yearly Av. Salinity			7·2	3·9		

* Drought.

sea in summer and colder than the sea in winter. This may be one reason for the seasonal changes in the migratory fish fauna.

In the same way there are large seasonal differences in salinity at the top of the estuary. Thus the average high-tide figures for Westford Bridge are $15{\cdot}9^{\circ}/_{\circ\circ}$ in winter and $27{\cdot}5^{\circ}/_{\circ\circ}$ in summer, at the Old Drift the figures are $1{\cdot}3^{\circ}/_{\circ\circ}$ and $16{\cdot}5^{\circ}/_{\circ\circ}$ and at the Charlesford Rapids $0{\cdot}3^{\circ}/_{\circ\circ}$ and $10{\cdot}7^{\circ}/_{\circ\circ}$. Low tide figures show small seasonal differences.

The salinity averages are based on few records, and the differences quoted may be due to unusually heavy rains or droughts in the period just before the samples were collected. Table II includes such records. Thus the effect of a low rainfall (0·72 inches) in March 1949 is reflected by abnormally high salinities in the middle of April at Charlesford Rapids, the Old Drift, and Westford Bridge. Similarly, the effect of a high rainfall (5·53 inches) in July 1947 was shown almost immediately in lowered salinities at the Old Drift and Westford Bridge, and in fact right down to Fountain Point. Due to the small size of the drainage basin, the salinities appear to change rapidly after unusual conditions of rainfall.

Although the seasonal averages are suspect for these reasons, it will be noted that along the whole estuary (with one exception at Fountain Point) the average summer salinity is higher than the average winter salinity. The rainfall, on the other hand, is lower in winter than in the summer, so that high summer salinities cannot be due to low rainfall. The high summer salinities are more probably due to the higher temperatures causing greater evaporation.

On the suggestion of Dr. G. Deacon, the rates of evaporation in winter and summer were computed for the various stations along the estuary, using the formula $E = 3{\cdot}7(e_w - e_a)u$ given by Sverdrup, Johnson, and Fleming (1942), p. 120. The amounts of evaporation for six months at each station in summer and winter are compared with the salinities at the same stations and in the same seasons below.

Distance of station from sea (miles) . . .	0·4	2·6	3·4	6·1	9·7	10·7	11·8
Summer evaporation (in cm. of water lost) . .	21·2	22·2	23·3	23·1	25·9	25·9	31·0
Winter evaporation (in cm. of water lost) . . .	21·2	20·6	20·2	21·1	19·6	19·6	17·8
Summer salinity ‰ . .	35·4	35·5	33·5	35·5	23·3	14·5	7·9
Winter salinity ‰ . .	34·8	31·2	29·5	28·5	14·9	2·3	0·4

From these figures it is evident that there is little seasonal difference in evaporation in the lower half of the estuary due to the stable water temperatures there. At the top of the estuary there is quite a large seasonal change in temperature, and the rate of evaporation during the warm summer months then boosts the salinity to higher values.

B. *Tidal Differences.*—A comparison of tidal differences of temperature does not show anything of importance. Tidal differences in salinity are more interesting and are best marked in the upper reaches. In Table III the individual records have been averaged for each station. In the same table are included records of substratum, estimations of current strength, the number of benthonic species collected at each station, and the occurrence of certain faunistic components. These will be discussed later.

C. *Differences along the Estuary.*—As has been previously remarked, the temperature changes gradually along the length of the estuary, with the maximum seasonal changes at the top and occasional very low temperatures at the mouth in summer. The salinities show only slight reductions from the normal sea value of 35·7‰ along the first six miles but thereafter there is a marked decline, and minimum values are recorded at the top. Moreover, there are marked tidal differences in salinity at the top of the estuary, so that an animal living there is not only subjected to a reduced salinity but also to a variable one, whereas an animal living near the mouth has a constant salinity similar to that of the sea.

The Cold Sea Current.—According to Isaac (1937), records based on 1933 and 1934 give a mean annual sea temperature at Knysna Heads of 16·8° C., with a maximum monthly temperature of 19·85° C. in February and a minimum of 13·5° C. for August. In spite of this, very low temperatures are occasionally recorded on the Knysna coast in summer. We

TABLE III.—THE CHANGES IN PHYSICAL CONDITIONS AND BENTHONIC SPECIES ALONG THE ESTUARY. SALINITY, TEMPERATURE AND pH VALUES HAVE BEEN ABSTRACTED FROM TABLE II. THE CATEGORIES OF BENTHONIC ANIMALS ARE EXPLAINED IN THE TEXT.

Station.	Fountain Point.	Brenton and Paarden Is.	Rail Bridge.	The Point.	West-ford Bridge.	Old Drift.	Charles-ford Rapids.
Distance from the sea in miles	0·4	2·6	3·4	6·1	9·7	10·7	11·8
Average high tide Salinity °/₀₀	35·7	34·8	29·9	33·2	21·7	13·5	7·2
Average low tide Salinity °/₀₀	34·5	31·5	31·3	28·4	16·5	8·8	3·9
Average summer temp. °C. (excluding cold current)	20·8	21·4	22·6	22·1	24·0	24·4	27·7
Average winter temp. °C.	15·3	14·9	14·3	15·4	14·3	14·3	12·6
pH high tide/low tide	8·4/8·3	8·5/8·5	..	..	8·2/8·1	8·0/7·4	7·2/6·8
Main type of substratum	rock	muddy sand	muddy sand	sandy mud	mud	sand and rock	sand and stone
Rough estimate of current strength (m.p.h.)	strong (4·5)	fair	fair	fair (3·5)	weak (0·85)	weak	variable (0·43)
Number of benthonic species collected	133	113	61	61	28	16	22
Number of "typical sea-shore species"	63	25	19	12	3	1	0
Number of "estuarine species"	1	14	15	13	7	5	3
Distribution of "brack-water species"	0	3	0	1	6	6	19

ourselves recorded 11·5° C. on 2/3/48 and 11·0° C. on 5/1/50. According to local residents, these low temperatures are due to a very cold inshore current which appears after a south-east onshore wind has been blowing for a few days. The phenomenon has been described by Smith (1949), but its cause is as yet unknown. As reported by Smith, fish are often trapped on the shore and later found numbed in pools. When the cold water enters the estuary with the rising tide, it drives the fish before it. As it progresses upstream, it mixes with the warmer estuarine water and the temperature rises. With the ebb-tide the cold water moves downstream again. This is

shown in Table II by the records for 2/3/48 and 5/1/50 which have been brought together in Table IV.

Table IV.—Temperature Records extracted from Table II to illustrate the Extent to which the Cold Current penetrates up the Estuary. Summer Averages are shown for Comparison.

Distance from sea in miles.	0·4	2·6	3·4	6·1	9·7	10·7
High- and low-tide temperatures on 2/3/48 (°C.).	11·5 16·2	.. ..	17·4 21·3	22·0 23·5	22·5 25·9	23·2 26·7
High- and low-tide temperatures on 5/1/50 (°C.).	11·0 16·6	11·5 24·0	.. ..	17·0 24·1	27·0 27·0	29·0 27·5
Summer averages excluding cold current (°C.).	20·8	21·4	22·6	22·1	24·0	24·4

This shows that the cold water penetrates at least 6·1 miles upstream. The effect of this cold current seems to persist for a few days as shown by the following records taken by Mr van Dort at Thesen's Wharf.

Date (Nov. 1949)	14th	15th	16th	17th	18th	19th	20th	21st	22nd
High Tide, °C.	19·0	20·0	17·0	15·5	16·0	..	..	18·0	21·0
Low Tide, °C.	22·5	18·5	17·0	17·5	17·5	..	..	19·5	21·5

Records of pH.—The few records of pH are given in Table II, and averages are shown in Table III. The figures are very constant up to the Rail Bridge (3·4 miles from the sea), as might be expected from the high salinities and free circulation. At the Old Drift (10·7 miles from the sea) the average low-tide salinity falls to 8·8°/₀₀ and the pH drops to 7·4. At the Charlesford Rapids the salinity at low tide is about 3·9°/₀₀ and the pH is 6·8. The fresh water above the Rapids is reported by the Department of Inland Fisheries to be acid.

Turbidity and the Substratum.—The fresh water entering the top of the estuary from the river is normally free from silt but is stained brown with peaty matter. As noted in the Hermanus estuary by Scott, Harrison, and Macnae (1952), this brown colour is not salted out when mixed with sea-water, and even down at Thesen's Wharf, where the salinity is high, the brown colour is still faintly perceptible on calm days.

In the upper part of the estuary a certain amount of silt is stirred up by waves on windy days, but lower down the bottom is often visible through ten feet of water. At Fountain Point the water is always clear. The clarity of the Knysna estuary is in marked contrast with conditions found in the majority of South African estuaries where erosion in the upper reaches

produces a muddy estuary. It is probable that the clarity of the Knysna water is largely responsible for the luxuriance of the submerged vegetation and the richness of the fauna.

The substratum changes quite regularly along the length of the estuary in relation to the strength of the currents. As might be expected, the Charlesford Rapids run over pebbles and sand into a string of sandy pools. This condition continues as far down as the Old Drift, where a slight weir is formed by the rocky foundations of the drift. Below this the intertidal banks rapidly change to soft, black, oozy mud. Sand-spits are absent, and rocks only occur where they have been placed by human agencies as at the foundations of the bridge and along the road embankment. None the less it should be noted that a suitable substratum exists for a rock fauna. Dredging proved that the channel bed along this stretch is soft mud. This muddy substratum continues with little change from Westford Bridge down to Belvedere. Here the first banks of muddy sand are found on the sides of the main channels, and soft mud is restricted to the backwaters. At The Point the proportion of sand increases, and the first mid-channel sand-bank is found slightly lower down opposite Salt River. As before, stone is still restricted to the road embankment and the foundations of the rail bridge. Below the rail bridge, the channel bottom and most of the intertidal banks are muddy sand. Clean, loose sands are first found along the sides and on the bed of the main channel at Leisure Isle; the only rocks in this stretch are those built into the foundations of Thesen's Wharf and the causeway to Leisure Isle; the first natural rocky outcrops are below Leisure Isle. At first they alternate with patches of sand but at Fountain Point the whole shore is rocky and sand is limited to tiny coves.

The Faunistic Divisions of the Estuary.

The main physical changes along the length of the estuary have been described, and it is felt that the distribution of the benthonic animals must be related to them. The pertinent data is summarised in Table III and illustrated in text-fig. 2. Some authors have stressed the importance of salinity as a determining factor, others the substratum. Fresh-water biologists use current strength, and many biologists have remarked on the effects of temperature and pH. There is no doubt about the importance of all these factors in different estuaries, but the view taken here is that the environment must be considered as a whole and any one factor only becomes important when the limits of tolerance for that factor are reached. On this basis one might say with MacGinitie (1935) that attempts to determine faunistic regions within an estuary are of little value. But this is not so. The variations of the different factors are not haphazard

nor independent. Changes in current strength, substratum, and salinity vary harmoniously, and though there are many exceptions to the general scheme there is no doubt that the fauna does change in a logical way as one progresses from the top to the mouth of an estuary. Indeed the discovery of a sand fauna on the banks of a swift-flowing narrow channel in the upper reaches, of mud-dwellers in a backwater near the mouth, or of rocky-shore forms on the clean wave-splashed pylons of a bridge, merely strengthen the general principles.

On the basis of Table III the following broad divisions of Knysna estuary seem logical:—

I. *Knysna Heads*, including the rocky coast in the region of Fountain Point. Average salinity above $34{\cdot}5^{\circ}/_{\circ\circ}$, substratum rocky or clean sand, current strong, wave action fair, little variation in seasonal temperature, clear water, pH above 8.

II. *The Lagoon*, including Leisure Isle, Thesen's Wharf, the Rail Bridge and The Point. Average salinity above $28{\cdot}4^{\circ}/_{\circ\circ}$, substratum muddy sand, current fair, wave action nil, temperature higher than the sea in summer, slightly lower in winter, pH above 8.

III. *The Westford Channels*, from Eastford, past Westford Bridge to the Old Drift. Salinity average variable, between $8{\cdot}8^{\circ}/_{\circ\circ}$ and $21{\cdot}7^{\circ}/_{\circ\circ}$, substratum soft mud, current weak, wave action nil, temperature higher than the sea in summer, slightly lower in winter, pH usually above 8.

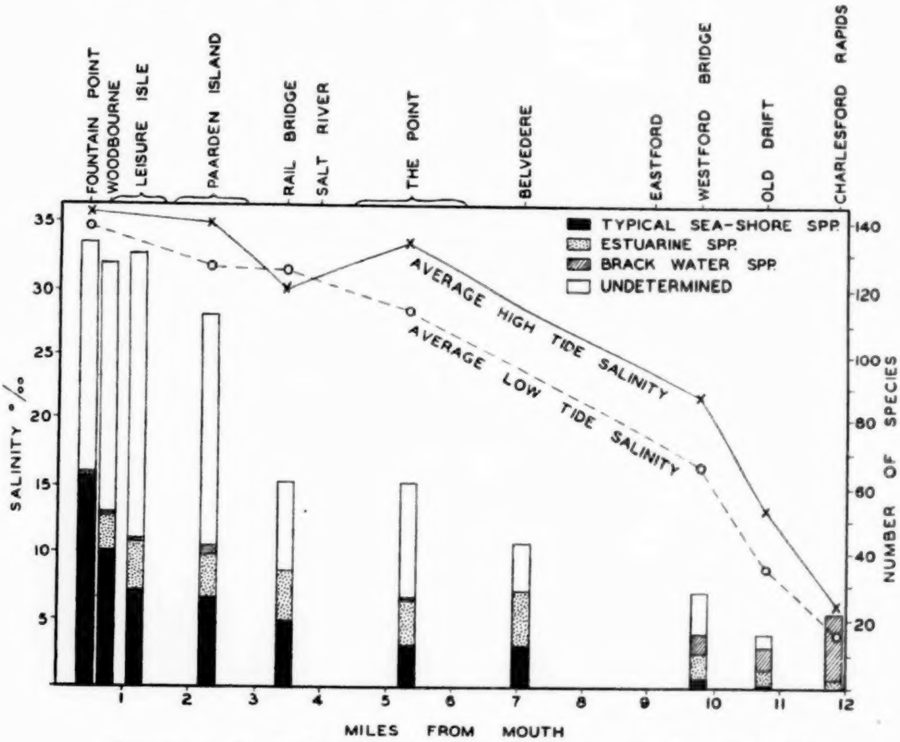
IV. *Charlesford Rapids*. Salinity very variable but except during droughts below $8^{\circ}/_{\circ\circ}$, substratum pebbles and sand, current variable, wave action nil, temperature very seasonal, pH below 8.

Reference to Table III shows how the different faunistic components fit in with these divisions which are based on physical characteristics. Text-fig. 2 illustrates the same figures diagrammatically.

First the "number of benthonic species collected". The figures in Table III are the totals from each station of the benthonic species listed in the Appendix, with the omission of Sponges and Tunicates, which have not yet been identified. We do not suggest that we have collected every species which occurs at each station, but we do feel that further collecting would not change the relative numbers.

As they stand, the figures show large numbers of species towards the seaward end of the estuary, and progressively smaller and smaller numbers upstream. The roughly similar totals at Fountain Point and Paarden Island suggest at first sight that this stretch is one faunistic region. But if the totals are similar, the component species show a marked change below Leisure Isle. Thus, over half the species recorded from Fountain Point do not reach Leisure Isle, and three-quarters of those found on Paarden Island do not extend down to Fountain Point. On the other

hand, the species recorded from Leisure Isle, Paarden Island, the Rail Bridge and The Point are essentially the same. On this basis, then, the lower part of the estuary has two faunistic divisions, namely Fountain Point and the stretch from Leisure Isle to The Point.



TEXT-FIG. 2.—The distribution of the faunistic components along the length of the estuary. The graphs for the average high- and low-tide salinities are plotted on the same figure. Based on figures from Table III.

Second, the "number of typical seashore species". The difficulty here was to avoid bias. Stephenson in 1944 drew up a list of common animals on the rocky shores of the South African coast, restricting himself to relatively large forms which could easily be observed on the shore. Any one of these occurring in Knysna estuary has thus been considered as a "typical seashore species". In all, 74 of Stephenson's species occur in the estuary, of which 63 or 85 per cent. are found at the rocky wave-washed Fountain Point and smaller numbers at other stations upstream. It is

clear that there is an abrupt decrease after Fountain Point and a progressive reduction higher up. Only one species reaches the Old Drift and none reach Charlesford Rapids.

The third group we have named "estuarine species". It soon became obvious that the majority of the animals in Knysna estuary are different from those which occur on rocky seashores. We could have made a list of estuarine species by simply comparing the Knysna lists with those from the seashore which we have built up during the last eighteen years. But we felt that this would not be wise, because in our shore work we have concentrated on large forms, and again we still know very little of the shallow-water fauna round the South African coasts.

Since we started the Knysna survey we have visited about thirty other estuaries, so we now know which species commonly occur in estuaries. We have therefore selected from the Knysna lists eighteen large species which occur commonly in estuaries and which do not occur on the shore except as very rare individuals (e.g. *Hymenosoma orbiculare*).

It may be that later, when we have completed the survey of Langebaan and Durban Bay, which are sheltered arms of the sea with a substratum of muddy sand, we shall have to revise our list of estuarine species or give it a different name. But it will not alter the fact that the eighteen species we have selected here all occur commonly in estuaries. The distribution of the eighteen "estuarine species" given in Table III and illustrated in text-fig. 2 again shows an abrupt increase upstream from Fountain Point and a decrease above The Point.

Finally, there is the fauna of Charlesford Rapids. None of the marine and only three of the "estuarine forms" extend into this stretch, and an analysis of its remaining fauna, which consists mainly of small crustacea, insects, and molluscs, shows that the bulk of the nineteen component species do not extend farther down than Westford Bridge. This group of animals undoubtedly has its centre of distribution at Charlesford Rapids. The term "oligohaline species" would be very useful here, but it has been used to categorise a slightly different salinity range. We have called them "brack-water species" in the table.

The species which make up the three last-mentioned components are not listed in full, but are indicated by symbols in the Appendix at the end of the paper. It will be noted that they amount to approximately one-third of the total number of species recorded. We have limited the discussion to these, because they are large, common, or belonging to clear-cut groups. Many of the others are small or rare, and in the present state of our knowledge we have not attempted to classify them.

The case for the faunistic divisions in the estuary could be strengthened by reference to particular groups of animals such as the amphipods, which

show a succession of replacing species along the length of the estuary, or by the inclusion of the fishes and plants, but this is hardly necessary. The four faunistic divisions are quite clear. *The Heads* have a marine rocky-shore fauna most of which is restricted to this area by the type of substratum and the wave action. *The Lagoon* has a fauna which is partly marine and partly estuarine. It includes many marine species which prefer sheltered waters and a bottom of sandy mud. These are prevented from spreading farther up the estuary by the change in substratum from sandy mud to soft mud and by the drop in salinity. *The Westford Channels* have a fauna almost entirely limited to estuarine forms, which prefer a muddy bottom and tolerate the lowered salinity. *Charlesford Rapids* have a very distinctive though restricted fauna, and the limiting factor is the low salinity.

These faunistic divisions will therefore be used in the general description of the estuary.

One interesting point remains. This is the effect of *tidal* differences in salinity on the distribution of animals along the estuary. The animals living at the top of the estuarine shore are only subjected to the high salinities of the flood-tide, whereas those lower down have to endure both the low salinities of the ebb and the variation of salinity from high to low tide. In view of this, it is conceivable that marine animals which live at the high-tide mark may extend farther up the estuary than those which live at lower levels. To test this suggestion the distribution and zonation of the 74 "typical seashore animals" listed in Table III was examined.

If the intertidal zone is divided into three rough vertical levels namely, upper shore, mid shore, and lower shore, and each of the 74 species classified according to the level at which it lives, it is found that five species live on the upper shore, twenty-two on the mid shore, and forty-seven at the lower levels. The distribution of these three groups along the estuary was extracted from the Appendix and summarised in Table V below.

TABLE V.—THE DISTRIBUTION ALONG THE ESTUARY OF TYPICAL SEASHORE ANIMALS INHABITING DIFFERENT LEVELS OF THE INTERTIDAL ZONE.

Distance from sea (miles)	0·4	0·7	1·1	2·6	3·4	6·1	8·0	9·7	10·7	11·8
Upper level-number .	3	3	3	3	3	2	3	2	1	0
% of total (5) . .	60	60	60	60	60	40	60	40	20	0
Middle level-number .	19	18	16	10	12	6	8	1	0	0
% of total (22) . .	86	82	73	45	55	27	36	5	0	0
Lower level-number .	41	19	9	12	3	4	0	0	0	0
% of total (47) . .	87	41	19	26	6	9	0	0	0	0

This shows quite closely that those marine animals which inhabit the upper levels of the shore penetrate further up the estuary than those which live at the bottom of the shore.

Vertical Zonation.

The terminology of the vertical zones on South African shores was worked out by Stephenson, Stephenson, and du Toit (1937). In a more recent paper, Professor Stephenson (1949) has reviewed this terminology and proposed one which can be applied universally. Among other changes he suggests that the term "sublittoral fringe", previously used to denote the lowest level of the South African shore visible between waves, should be replaced by "infralittoral fringe". We feel that the term "littoral" which has been used not only for the shore between tide marks but also for the whole of the shore plus the shallow sea is ambiguous. The term "infralittoral" is also suspect. We suggest that the shore between the tide marks should be termed the "intertidal zone" and indeed this is already widely accepted. We suggest in addition that the fringe of the sea-bed below the intertidal zone should be referred to as the "infratidal fringe". In brief, the part once known as the "sublittoral fringe" is best called the "infratidal fringe".

Although vertical changes in physical factors in Knysna estuary have not been investigated there is an obvious vertical zonation in both plants and animals. On the rocky shores of the Heads the normal seashore zones are evident, though the elimination of *Patella cochlear* above Fountain Point means that the limits of the "Cochlear Zone" are difficult to discern. Higher up the estuary the seashore zones disappear, and the vertical succession of plants is the best guide to the particular level on the shore at which one is working. At the highest levels of spring tides there are two dominant species. One is the small rush *Juncus kraussii* which is most common on black mud where the salinity is definitely below that of sea-water. The other is *Salicornia meyeriana* which appears to be able to stand high salinities and to grow even on sand. One or other of these plants always occupies the uppermost level of the shore except on rocky stretches.

Slightly lower down, the rice grass *Puccinella fasciculata* is abundant. It is common on the seaward side of the causeway to Leisure Isle, small stands occur on the sandy point of the island, and denser growths are found on Paarden Island and as far up as Ashford. Higher up along the Westford Channels it is scanty, and the mud below the *Juncus* level may either support a little *Cotula coronopifolia* or is completely bare until the *Zostera* level is reached.

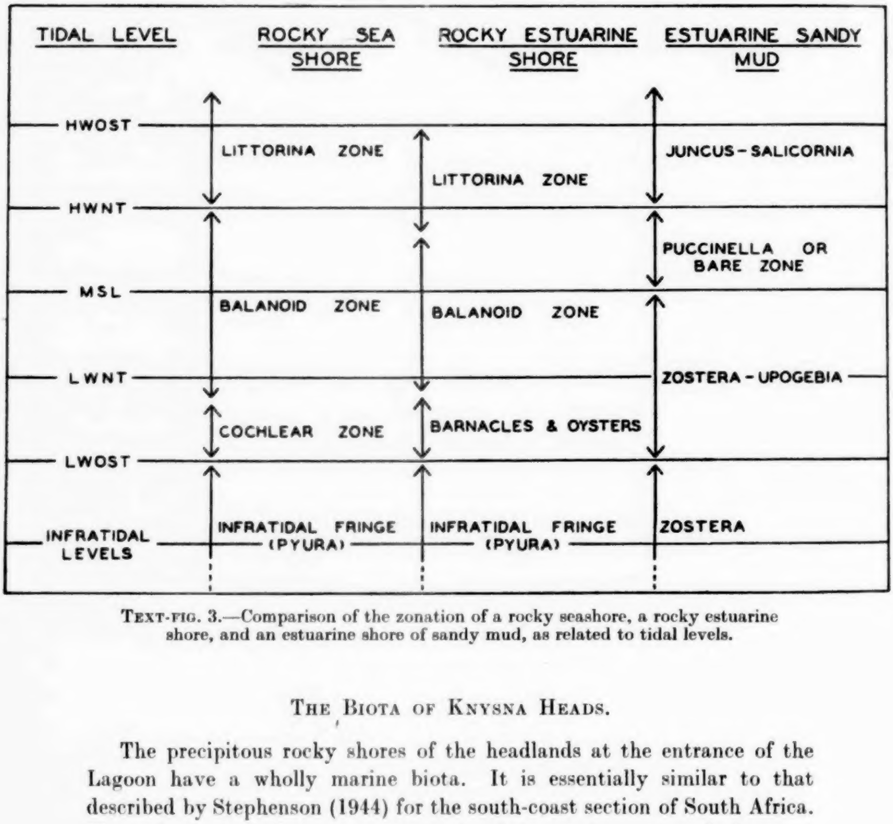
From mid-tide down to the lowest level of spring tides, and even below this, the dominant plant is the sea-grass *Zostera capensis*, which to all but the expert is indistinguishable from the world-wide *Zostera marina*. It grows all over the estuary from Leisure Isle to the Old Drift, being most luxuriant at low water of springs on a shelving mud-bank in a salinity of about 30 parts per thousand. Where the mud-banks are flat and water-logged, as on parts of the Brenton and Belvedere shores, it is mixed with or largely replaced by another estuarine flowering plant *Halophila ovalis*. Below the tide mark in the lower half of the Lagoon several algae occur in the *Zostera* beds, and among these *Zonaria tournefortii* is particularly common. Above Westford Bridge and at the Old Drift *Zostera* is mixed with *Ruppia* sp. Along the Charlesford Rapids *Zostera* is absent and *Ruppia* is of local occurrence. The aquatic *Scirpus globiceps*, which is of fresh-water origin, is common in the upper parts of these rapids.

The rocky banks of the estuary have the same sort of zones as occur on an open rocky shore, but many of the common shore forms are absent and others are replaced by estuarine species. On the piles of Thesen's Wharf, *Littorina knysnaensis* occupies the highest levels; below this are barnacles (mainly *Balanus amphitrite* var. *denticulata*); lower down there are mussels (*Mytilus perna*) and a few oysters (*Ostrea* (*Gryphaea*) *margaritacea*); and at the lowest spring tides a few sea-squirts (*Pyura stolonifera*) may be visible. On the Rail Bridge the fauna is much more scanty. The mussels have gone and the barnacles are reduced in numbers. Higher up the estuary the rock fauna is reduced even further. *Pyura* disappears, then oysters become rare and finally even the Littorina zone is affected. At Westford Bridge *Littorina knysnaensis* is largely replaced by *Assiminea* sp. Below this level the estuarine barnacles *Balanus amphitrite* var. *denticulata* and *B. elizabethae* have completely replaced the shore species. The estuarine mussel (*Modiola capensis*) occurs with them and extends below the tide marks. At the Old Drift the upper rocks are colonised by *Assiminea* sp., and below these are *Balanus elizabethae* and *Modiola capensis*. In the Charlesford Rapids vertical zones are no longer distinguishable.

A rough comparison between the zonation of a rocky seashore and the rocks or sandy mud-banks of Knysna estuary is given in text-fig. 3 and will make the whole position clearer. The relation between zones and tidal levels is not exact, but is still accurate enough to give a fair impression to one not acquainted with the normal zones on South African shores.

Against the background of the physical changes along the estuary, the faunistic divisions, the vegetation, and the vertical zonation, we can now describe the biota of the whole estuary. No attempt will be made to describe the biology or the distribution of all the recorded species. In many cases we could give no more than a few scrappy notes. We have therefore

summarised the records of distribution and abundance as shortly as possible in the Appendix. But there are a certain number of common species which we have studied in some detail. These give character to the different faunistic divisions of the estuary, which we shall now describe.



TEXT-FIG. 3.—Comparison of the zonation of a rocky seashore, a rocky estuarine shore, and an estuarine shore of sandy mud, as related to tidal levels.

THE BIOTA OF KNYSNA HEADS.

The precipitous rocky shores of the headlands at the entrance of the Lagoon have a wholly marine biota. It is essentially similar to that described by Stephenson (1944) for the south-coast section of South Africa. The animals and plants are present in their usual zones, and the most obvious feature is a progressive reduction in the richness of the fauna as one penetrates into the Lagoon. This is very striking at Fountain Point. It is hard to believe that this change is due to the very slight reduction in salinity. More probably it is caused by the obvious reduction in wave action and to the increase in sand. This may be exemplified by the case of *Patella cochlear*, and here it may be helpful to add a few notes to Stephenson's description of the open seashore in the vicinity of Knysna. Stephenson

(1939 and 1944) has shown that *P. cochlear* requires a moderate amount of wave action. On very exposed reefs it is replaced by barnacles (particularly *Octomeris angulosa*) and mussels (*Mytilus perna*), and in sheltered coves it is replaced by an algal carpet. Within recent years we have visited several localities near Knysna such as Keurboom Strand, Buffalo Bay, and Glentana Strand, where the foreshore is sandy and the lower beach rocky. In such situations *Ostrea* (*Gryphaea*) *margaritacea* Lamarck (referred to in Stephenson's papers as *O. iridescens* Gray) is so abundant that it is exploited commercially. This oyster extends down from the middle of the Balanoid zone well into the Cochlear zone, particularly on rocks which are liable to be covered at intervals by shifting sands.

These same oysters occur in small numbers on Knysna Heads. As one progresses upstream towards the Lagoon it is noticeable that *Patella cochlear* is becoming more and more rare. It occurs only on the seaward faces of clean rocks and is replaced by the algal carpet on flattened reefs or by the increase and downward extension of oysters in sandy places. This is particularly obvious on Brenton Head where the oysters have not been disturbed. Upstream from Fountain Point, *P. cochlear* is entirely absent, and towards Woodbourne (on the east bank below Leisure Isle) good oyster-beds would grow were they not hacked off by every picnic party.

This Woodbourne stretch of shore is interesting in other ways. It is particularly poor in those species which one expects at the low-tide mark on an open seashore. This is probably due to the nature of the shore, which is strewn with small loose boulders. Occasionally, where suitable shelter is provided, as on the piles of a jetty, a rich fauna is present. On the other hand, the Littorina zone is little affected. *Littorina knysnaensis* itself, *Thais dubia*, *Oxystele variegata*, and the crab *Cyclograpsus punctatus* are present in normal numbers. In the Balanoid zone there are considerable changes. The barnacle *Octomeris angulosa* has disappeared with the absence of wave action; *Chthamalus dentatus* and *Tetraclita serrata* remain fairly common and to these are added a few specimens of two estuarine barnacles, *Balanus amphitrite* var. *denticulata* and *Balanus elizabethae*. Limpets have mostly disappeared; *Patella oculus* is the only one present in any numbers; *P. granularis* and *P. miniata* have isolated representatives. *Helcion pectunculus* is rare, but *Siphonaria* spp. flourish. Many species of the snail-like molluscs have gone, but *Oxystele variegata* is still common, and there are surprisingly large numbers of *Oxystele tigrina* and a few *Cominella cincta*. There are also fair numbers of chitons (*Acanthochiton garnoti*), a single anemone (*Pseudactinia flagellifera*), the starfish *Asterina exigua*, and among Polychaets the common *Pomatoleios crosslandi* and *Thelepus plagiostoma*. The great bulk of the algae are absent, leaving only a few tufts of *Gelidium pristoides*, *Ulva lactuca*, and *Enteromorpha* sp.

In what corresponds to the Cochlear zone, the changes are even more marked. *Patella cochlear* is replaced by a thick band of *Ostrea* (*Gryphaea*) *margaritacea*. With these are a few *Mytilus perna*, *Oxystele sinensis*, barnacles, and various small species living in crevices, but all the larger animals which flourish on an open seashore have gone and the macroscopic algae as well. This level has a very restricted fauna indeed.

Surprisingly enough, a few *Pyura stolonifera* persist at the very bottom of the shore in what we have termed the infratidal fringe and below.

Dredging in the channel between the Knysna Heads indicated again that the fauna is essentially marine and that there is a sharp reduction in the number of species upstream from Fountain Point. The reason is quite obvious. From the few hauls that were made it was clear that the channel bottom at Fountain Point is rocky and the fauna rich. A little farther up, the bottom is coarse sand and broken shells, and appears to be almost barren of the larger forms of life. Clean sand is an indication of an unstable bottom and a lack of organic detritus upon which many bottom dwellers depend for their food supplies. This type of substratum with its impoverished fauna is thought to be due to the strong tidal currents between the Heads.

On the under sides of buoys anchored in the channel just within the Heads was a rich growth of hydroids, polyzoa, and barnacles with numerous epizootic species of polychaets, isopods and amphipods.

To summarise then, these inner rocks have a very poor but an essentially marine Littorina zone, next a reduced Balanoid zone, below this a band of oysters, and at the bottom a few *Pyura*. Algae are conspicuous by their absence and the rocks look very bare. Below the tide marks the swift currents allow the growth of a rich rock fauna, but where sand is deposited it is very barren.

The Biota of the Lagoon.

The lower limit of this division of the estuary is quite sharp. There is a sudden change from the essentially rock fauna of the Heads to the muddy-sand fauna of Leisure Isle. From here on conditions remain fairly uniform as one progresses up past the Brenton banks, Paarden Island, the Rail Bridge, and the mouth of Salt River to The Point. But the upper limit of the Lagoon is not well defined. Reference to Table III shows that the changes in physical conditions and biota are gradual. Possibly Belvedere and Eastford should be included in the Lagoon section. But while the banks of the main channels in this stretch are like those of The Point, there are great stretches of mud in the backwaters very similar to the Westford Channels, and for this reason The Point is regarded as the upper limit of

the Lagoon, and the Belvedere–Eastford stretch as an overlap between this section and the muddy Westford Channels.

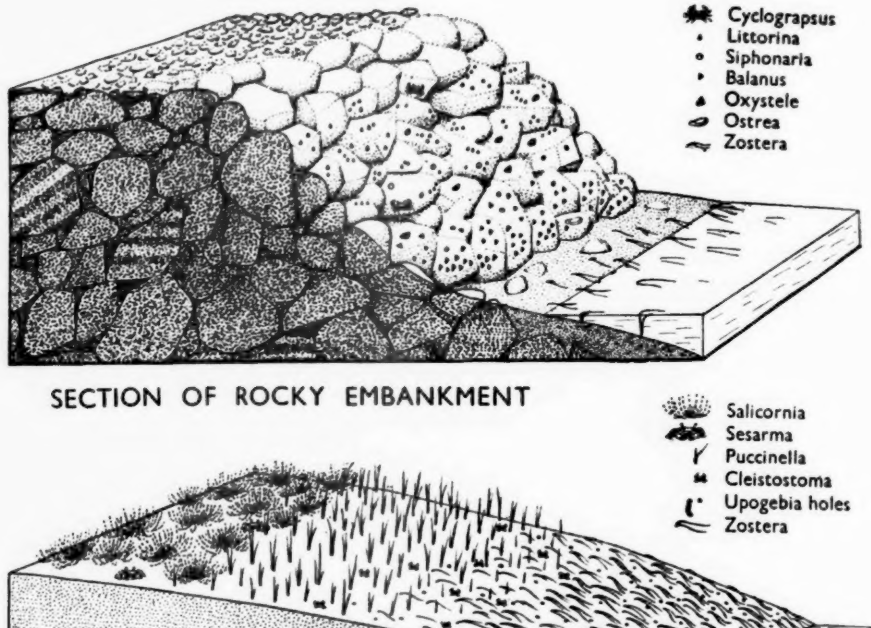
It has been mentioned that the majority of the characteristic animals and plants of this Lagoon live on or in muddy sand in conditions of high salinity. Each is restricted to a particular level. There is an obvious zonation of plants, and an equally good, though less obvious, zonation of animals. The two will be described together, and the main elements are shown in text-fig. 4.

The Juncus-Salicornia Zone.—On the banks between Paarden and Leisure Islands at the high spring-tide level there are extensive flats of *Salicornia meyeriana.* Growing with *Salicornia* are *Chenolea diffusa* on the better drained ridges, and *Triglochin elongatum* in the damp hollows. Among the many other plants are tufts of *Juncus kraussii* and the sea-thrift *Limonium linifolium.* The animal population of these salt marshes includes great numbers of crabs, particularly *Cyclograpsus punctatus* in the more sandy areas, and *Sesarma catenata* in the more muddy ones. *Ligia natalensis* creeps among the *Salicornia* roots, and amphipods such as *Cymadusa australis* swarm in *Enteromorpha*-covered pools. *Littorina knysnaensis* is found on rocks or attached to the stems of grasses; *Assiminea* sp. is common on the mud.

As the proportion of mud in the sand increases and the salinity falls in the stretches above the Rail Bridge, *Juncus* becomes more common and finally forms dense fields. With it the crab *Sesarma catenata* increases to enormous numbers. This then is the top level on the shore, a Juncus-Salicornia zone with a restricted fauna whose proportions vary with local conditions. It should be remembered that this is replaced by a normal Littorina zone where rocks occur.

The Puccinella or Bare Zone.—Away from the main channels and in the backwaters, *Salicornia* or *Juncus* mixes with the rice grass *Puccinella fasciculata* which occupies a slightly lower level on the shore. This may be seen on the sandy point of Leisure Isle or on Paarden Island. More often, however, the mud at the edge of the *Salicornia* or *Juncus* bed is eroded away, and a "salting cliff" is formed similar to that described by Hartley and Spooner (1938) for the Tamar estuary. In this case there is a stretch of bare mud before the *Zostera* level is reached (*cf.* text-fig. 4). *Sesarma* and *Assiminea* extend down wherever *Puccinella* provides shelter, but on the bare mud the small crab *Cleistostoma edwardsii* is the dominant form. It digs shallow burrows in the mud, and on The Point may reach a density of one hundred per square metre.

Where *Puccinella* occurs in the neighbourhood of rocks it may be seen that its level corresponds with the upper Balanoid zone in which the barnacles *Balanus amphitrite* var. *denticulata, Balanus elizabethae,* and *Tetraclita*



TEXT-FIG. 4.—Diagrammatic representation of the main types of plants and animals living on the shore at the top of the lagoon. Three types of bank are shown, and the water-level represents low tide of springs.

serrata are the dominant forms. *Oxystele variegata* extends down from the Littorina zone, and there are also many *Siphonaria oculus*, an occasional starfish (*Asterina exigua*) or chiton (*Acanthochiton garnoti*), and in one locality on the Salt River embankment a surprising number of the subtropical gastropod *Nerita albicilla*. Indeed, it seems probable from our work on other estuaries that warm-water species extend farther south in estuaries than they do on the open seashore. Reference to Table III, which shows higher temperatures in the Lagoon than in the sea, seems a reasonable explanation for this.

The Zostera-Upogebia Zone.—In some places *Puccinella* extends down to the middle of the shore and mixes with *Zostera capensis* extending up from below. The junction is often marked with a narrow band of the green alga *Ulva* sp. When *Puccinella* is absent, a few stunted *Zostera* plants on bare mud mark the upper limit of the zone. *Zostera* extends down to about three feet below the spring tides, but the other animals and plants which are found on the lower half of the shore do not have the same vertical range. However, the holes of the burrowing prawn *Upogebia africana*, locally known as the "copper shrimp" or "mud prawn", are abundant over the whole Lagoon from mid-tide to low water of springs and provide a simple basis for determining levels when working on the shore. The lower level of the zone is thus marked by the distribution of *Upogebia*.

Zostera and *Upogebia* are abundant wherever sandy mud occurs. Where the bottom changes to clean sand, as along the edges of the channel opposite Leisure Isle, *Zostera* becomes scanty and *Upogebia* is replaced by another burrowing prawn *Callianassa kraussi*. On soft mud *Zostera* remains abundant, but *Upogebia* is scarce. *Zostera* and *Upogebia* are most abundant at low tide having a water table six inches below the surface. Where the banks are very flat and waterlogged, a second flowering plant *Halophila ovalis* occurs, and the pistol shrimp *Alpheus crassimanus* makes long branching galleries among its roots. The common goby (*Gobius nudiceps*) finds shelter in these at low tide.

Many small surface animals shelter among *Zostera*. The crab *Cleistostoma edwardsii* extends down from upper levels, and a second crab *Hymenosoma orbiculare* makes its home here. There are also dozens of hermits (*Diogenes brevirostris*), two common whelks (*Nassarius kraussiana* and *Natica imperforata*), the tectibranch *Haminoea alfredensis*, the goby *Psammogobius knysnaensis*, shrimps (*Leander pacificus*), isopods (*Paridotea ungulata* and *Exosphaeroma hylecoetes*), and many amphipods including *Cymadusa australis*.

On digging below the surface, many burrowing forms apart from *Upogebia* are found. The commonest of these are the bivalves *Loripes clausus* and *Solen capensis*, the polychaets *Marphysa sanguinea* and *Lumbri-*

conereis tetraura and the holothurian ***Epitomapta knysnaensis***. The giant *Arenicola loveni*, locally known as the "blood worm", is dug with difficulty. It may reach a length of twenty-four inches and the thickness of one's thumb. Unlike most species of the genus, the hole is not marked by sand casts but by a shallow funnel-like depression below which the burrow extends down a good three feet, the upper part being blocked by a core of unexpelled sand.

In order to determine the relative abundance of the commoner species under varying conditions in different parts of the Lagoon, a square metre was dug up at different points and the common large animals counted.

Station 1 was muddy sand off the point of Leisure Isle below mid-tide, water table at 10–11 inches.

Station 2 was muddy sand near Thesen's Wharf below mid-tide, water table at 6 inches.

Station 3 was muddy sand on The Point below mid-tide, water table at 6 inches.

Station 4 was soft mud at Belvedere below mid-tide, water table at 2 inches.

TABLE VI.—THE ABUNDANCE OF BURROWING ANIMALS AT DIFFERENT STATIONS IN THE LAGOON AS SHOWN BY COUNTS IN AREAS OF 1 SQ. METRE EACH. (See also description in text.)

Species.	Station 1.	Station 2.	Station 3.	Station 4.	Total.
Zostera capensis	Common	Abundant	Abundant	Abundant	
Cleistostoma edwardsii	80	14	37	33	164
Hymenosoma orbiculare	9	3	0	4	16
Upogebia africana	153	74	117	1	345
Loripes clausus	48	62	50	4	164
Solen capensis	0	0	1	0	1
Epitomapta knysnaensis	3	6	0	0	9
Marphysa sanguinea	9	12	4	12	37
Lumbriconereis tetraura	56	31	10	0	97
Total large animals	358	202	219	54	

It is evident that the Leisure Isle banks are richer than those upstream and that the fauna of soft mud is much poorer than that of sandy mud.

On piles and rocky banks at this lower level the fauna is poor. The larger algae are absent. The dominant animals are barnacles, particularly ***Balanus** amphitrite* var. *denticulata* and *B. elizabethae*, and oysters (*Ostrea* (*Gryphaea*) *margaritacea*). *Mytilus perna*, though present in quantity on

the piles of Thesen's Wharf, is absent from the rocky embankments whose stones are covered with a thin film of mud. A few specimens of the estuarine mussel, *Modiola capensis*, grow in the rock crevices.

The Infratidal Levels.—The banks below low spring tides are difficult to work. Some forms can be collected by wading, particularly when a spring tide coincides with a wind blowing down the Lagoon. Abnormally low tides then occur. But quite a lot can be seen from a small boat when the water is smooth and clear. It has been mentioned that *Zostera* extends some three feet below tide marks, and at this level it is commonly mixed with the red alga *Zonaria tournefourtii*. This species is normally attached to low-tide rocks on the seashore, but here it seems to be very loosely attached to *Zostera*. A few animals also attach themselves to *Zostera* fronds. The anemone *Pseudactinia flagellifera* is the most conspicuous but there are also Didemnid ascidians (unidentified), polyzoans (*Bowerbankia pustulosa*), isopods (*Paridotea ungulata*), shrimps (*Hippolyte kraussiana*) and periwinkles (*Rissoa pinna*). Two conspicuous sponges, which are so far unidentified, a tubular white (KNY 17B) and a massive yellow (KNY 6T), are anchored in the sand among the *Zostera* plants, and here and there may be found groups of the horse-mussel *Pinna squamifera*.

Many forms crawl on the surface of the sandy mud. Crimson nemertines (unidentified) are conspicuous but uncommon. The crab *Hymenosoma orbiculare* and the bivalves *Cardium turtoni* and *Lima rotundata*, the gastropods *Turritella knysnaensis* and *Natica imperforata*, and the echinoid *Parechinus angulosus* are common. Here and there the giant tectibranchs (*Bursatella leachii*) may be found. Other species plough along just below the surface such as the gastropod *Cassis achatina* and the echinoids *Echinodiscus bisperforatus* and *Echinocardium cordatum*. (The former are locally known as "pansy shells".) The animals which make deeper permanent burrows are largely unknown, but from what we have seen they do not differ greatly from those between the tide marks.

It is obvious that these banks of muddy sand harbour a very rich fauna indeed, particularly those off the point of Leisure Isle and near the Brenton shore. There is no doubt that many new species await discovery.

Where the substratum changes to clean sand, as it does along the edge of the swift channel past Leisure Isle, the fauna becomes much poorer. *Zostera* disappears, and the main forms are the heart urchin (*Echinocardium*), the cake urchin (*Echinodiscus*), and the lob worm (*Arenicola*). Where it changes to soft mud, *Zostera* persists with its attached fauna but the burrowing forms disappear.

In the very few situations where infratidal rocks are not covered by mud (*e.g.* Thesen's Wharf and the Rail Bridge) all that could be seen was that sponges are common and that the large simple ascidian *Pyura*

stolonifera, so common on open seashores, still persists though the test is now delicate and the flesh pale.

The Results of Dredging in the Lagoon.—The fauna which has just been described is that found at or just below the low-tide mark. We know the fauna of the deeper waters only through the few dredge hauls we have made round Leisure Isle, Paarden Island, and in the channel from Salt River to Belvedere. We can only say that the bottom in this stretch of the estuary seems to be firm sandy mud covered with drifting weed. This weed shelters the same forms as are attached to *Zostera* at the low-tide mark with larger numbers of small *Parechinus* and amphipods. With the weed are tangled masses of the polyzoan *Bowerbankia pustulosa*, many species of hydroids, and in the side channel between Leisure and Paarden Islands the interesting *Hippocampus capensis*, known only from the Knysna estuary. We know nothing of the burrowing fauna as our dredge would not "dig in".

Above the Rail Bridge and opposite Salt River the dredge brought up many lumps of *Pyura* overgrown with *Bowerbankia*, in the meshes of which living *Turritella knysnaensis* were found attached. It is odd to find a gastropod attached like this, but the genus *Turritella* is known to be a ciliary feeder. Farther up the channel, opposite Belvedere, masses of living *Codium tenue* were brought up with many shrimps (*Leander pacificus* and *Hippolyte kraussiana*) clinging to it. There were also lumps of gluey mud containing the estuarine mussel *Modiola capensis*. The presence of these indicated that the top of the Lagoon had been reached, as this species is characteristic of the Westford Channels.

The Biota of the Westford Mud Channels.

This section of the estuary is some three miles long, extending from the upper part of Belvedere (Ashford Corner) past Westford Bridge to the Old Drift. The salinity is low and variable, the banks are swampy and overgrown with *Juncus*, and the channel is narrow, winding, and muddy. The fauna of the whole area is poor.

Juncus kraussii is the dominant plant at the top of the shore, and wide fields of it extend along the banks. *Salicornia*, *Chenolia*, and *Triglochin* occur at Westford Bridge and elsewhere. Reeds (*Phragmites communis*) are found below fresh-water springs and all of these plants mix with rank grasses on higher ground. Opposite Ashford there are fields of *Puccinella* below the *Juncus*, and higher up there are patches of *Cotula coronopifolia* in the side channels, but along the banks of the main channel there is a marked salting cliff at the edge of the *Juncus* fields and below this a stretch of almost liquid mud before the *Zostera* level is reached. The *Zostera*

continues below the low-tide mark. The characteristic zones are thus a Juncus zone, a Bare zone, and a Zostera zone.

The Juncus Zone.—Among the *Juncus* tufts there are great numbers of the crab *Sesarma catenata* but nothing else. On the rocky embankments at Eastford, *Sesarma* is replaced by *Cyclograpsus punctatus* and with it are *Littorina knysnaensis*, *Ligia dilatata*, *Siphonaria aspera*, *Oxystele variegata*, and *Thais dubia*, in fact all the normal inhabitants of a Littorina zone on a rocky seashore. Farther up at Westford Bridge, *Littorina*, *Cyclograpsus*, and *Ligia* still occur in small numbers, but at the Old Drift all have gone and *Assiminea* replaces *Littorina* at the top level of the shore.

The Bare Zone.—At this level *Cleistostoma edwardsii* and *Assiminea* sp. are the only common animals on the open mud. On rocky embankments *Oxystele variegata*, *Balanus elizabethae*, *Modiola capensis*, the estuarine isopod *Cirolana fluviatilis* and the amphipods *Parorchestia rectipalma* and *Melita zeylanica* are found in quantity under barnacle-covered rocks. Above Westford Bridge the last marine form, *Oxystele variegata*, disappears, and only barnacles, mussels, and isopods remain on the lower stony outcrops.

The Zostera Zone.—*Zostera* grows luxuriantly at the top of the Lagoon but becomes very patchy as one progresses up the mud channels. At Westford Bridge the first few plants of *Ruppia* sp. were found with the *Zostera* and at the Old Drift the two are equally common. The surface fauna of the *Zostera* beds consists of crabs such as *Cleistostoma edwardsii* and *Hymenosoma orbiculare*, several amphipods and isopods and loose balls of the green alga *Ulva* sp. containing the estuarine mussel *Modiola capensis*. The burrowing fauna is restricted to a few *Upogebia africana* and *Solen capensis* in the firmer mud, odd specimens of other bivalves, several minute polychaets, and one very large swimming crab, *Scylla serrata*. This is locally known as the "Knysna crab" and is regarded as a great delicacy. Fishermen report that it is caught only during the summer and that only males are found. It is gaffed from its holes in the *Zostera* beds or caught in hand-nets at night. Our own observations agree with these reports. We have taken large males from various points between Leisure Isle and Westford Bridge in summer, but only one small male in winter. The burrows are six to eight inches in diameter and extend horizontally some ten to twelve feet below the surface of the *Zostera*. They are also common in the sides of the salting cliff, but here they slant down to the permanent water-level where a larger den is formed into which the crab retreats during daylight. This crab is another tropical Indo-Pacific species found in estuaries from the Natal coast southwards. Although we have collected them from many estuaries at all seasons, we have never seen one in berry and believe that they migrate down to the sea to breed.

The Results of Dredging in the Westford Channels.—Dredging gave poor results. The bottom is soft mud with a good deal of decaying *Zostera*. The only common animal is *Modiola capensis*, probably attached to the surface in its natural state, but when dredged it appears as the centre of a mud ball.

The Biota of the Charlesford Rapids.

This stretch is about a mile long, consisting of a series of stony rapids linking long sandy pools. The water is stained brown, the salinity is very variable but generally below $10^\circ/_{oo}$, the temperature varies from 12° C. in winter to 28° C. in summer, and the tidal range is twelve to eighteen inches. The vegetation is a scanty growth of halophytes, and the fauna is composed of a few estuarine forms plus some salt-tolerant but essentially fresh-water species.

Above the Old Drift there is no obvious vertical zonation. Indigenous bush grows on the banks, and coarse grass extends to the water's edge. Here and there on the banks clumps of *Juncus* may be found, and the swampy areas are overgrown with *Cotula coronopifolia*, with patches of *Scirpus venustulus*, *Triglochin elongatum*, and *Juncus kraussii*. The upper pools are fringed with reeds (*Phragmites communis*). The submerged vegetation consists of rather scanty *Ruppia* sp. in the lower sandy pools, and the short, tufted *Scirpus globiceps* in the upper ones. The rapids themselves are very bare.

Animal life is scanty; all the species are small and, as might be expected, some are more common in the sandy pools and others in the stony rapids. Thus *Callianassa kraussi* is restricted to the lowest sandy pools and *Modiola capensis* is commonly attached to stones. The characteristic organism of the area is the isopod *Pseudosphaeroma barnardi*. Other isopods such as *Paramunna* n. sp., *Cirolana fluviatilis*, and *Cyathura carinata*, the tanaid *Leptochelia savignyi*, and amphipods such as *Corophium triaenonyx*, *Grandidierella lignorum*, and *Melita zeylanica* are common among stones. These all belong to the estuarine component. Species of fresh-water origin include a few Hydroptilid caddis larvae (e.g. *Argyrobothrus* sp.), chironomid larvae, the corixid *Sigara contortuplicata*, and the naiad of the dragon-fly *Orthretrum ? capense*.

Although the Appendix contains several more species, it is obvious that this stretch of the estuary has an impoverished and specialised fauna. The fauna of the pools higher up the river is typical of an acid fresh-water stream. The population is fairly dense and includes Baetid nymphs (common), nymphs of *Pseudagrion* (fairly common), tusk-shaped caddis larvae (numerous), nymphal Belostomids (fairly common), *Micronecta*

butleriana (fairly common), *Plea piccanina* (few), *Sigara contortuplicata* (few), and a small number of Dytiscids. It is noteworthy that only one of these, namely *Sigara contortuplicata* extends from the fresh into the brackish water of Charlesford Rapids.

Plankton.

We have concentrated on the benthon and its distribution in relation to physical factors. We felt that these relatively immobile forms are a better guide to the effects of changing conditions than the plankton which drifts to and fro with the currents or the nekton which can actively avoid unfavourable conditions. But we have not entirely neglected other forms of life. We have collected plankton ourselves and have received copies of the lists of planktonic diatoms prepared by the Division of Fisheries. We feel, however, that a lot more work must be done before anything more than a list of species can be published. So at present all we can say is that the plankton is rather poor. Previous writers have suggested that plankton is not very important in the economy of estuaries with the exception of the mysids. Surprisingly enough, we have obtained relatively few mysids from Knysna; two species off Leisure Isle and one near Belvedere and none of these was common. No doubt further work will show a richer fauna, but up to the present the mysid fauna of Knysna does not compare with that of the Keiskama or other muddy estuaries.

The Fish Fauna.

If the plankton is meagre, the fish fauna is certainly not. As might be expected from the luxuriant vegetation, the large amount of detritus, and rich bottom fauna, Knysna has an abundant and varied population of fishes. We ourselves have done a certain amount of netting, but our nets were small and the catches accordingly restricted to small species or the fry of larger ones. However, Professor J. L. B. Smith has worked on the Knysna fishes for many years and has seen all our specimens. We hope that he will describe the fish fauna of Knysna estuary.

Fishes and birds are the culminating links of most estuarine food chains, and we hope at a later stage to discuss the whole question of the economy of estuaries. We have collected a certain amount of data from Knysna for this purpose and are now actively engaged in collecting and analysing more material from other estuaries. This will form the subject of a separate paper.

Conclusions.

In this paper we have attempted to describe the conditions of life in Knysna estuary and the distribution of benthonic plants and animals. The interesting features of Knysna are the depth at the mouth, the evenness of the rainfall, the absence of silt in the river and the resulting clarity of the estuary. A large part of the lower estuary has a salinity almost equal to sea-water. At the same time, wave action is limited to the rocky Heads, and the Lagoon above is quiet and sheltered with stable banks of muddy sand. These conditions are very different from the wave-tossed seashore and it is not surprising that there is a sharp change in the fauna at Fountain Point. Above the Lagoon at The Point there is another change, this time a decrease in salinity and a change from muddy sand to soft mud. The whole fauna becomes impoverished from here on. Many burrowing forms disappear, and the last few marine forms drop out one by one.

A further change occurs at the Old Drift. The salinity drops to low values and becomes increasingly variable; the substratum changes from mud to sand and stones. In consequence the fauna is further restricted and more specialised. All the marine forms have gone, a few estuarine forms persist and to these are added some salt-tolerant fresh-water species.

The four faunistic divisions are thus determined by changes in wave action, salinity, and substratum, and variations in the latter are related to current strength. The divisions in an ideal estuary were given by Day (1951), and we are now in a position to compare these hypothetical divisions with what we have found at Knysna. The hypothetical divisions were:—

1. *Head of the Estuary.*—Salinity below 5°/oo, current variable, substratum variable.
2. *The Upper Reaches.*—Salinity 5 to 15°/oo, current weak, substratum mud.
3. *The Middle Reaches.*—Salinity 15 to 25°/oo, current fair, substratum muddy sand.
4. *The Mouth of the Estuary.*—Salinity above 25°/oo, current rapid, substratum clean sand or rock.

If this scheme is compared with the divisions of Knysna estuary given on p. 383, it will be seen that the same sequence of changes occurs but that the salinity figures do not agree.

The sequence of salinities are:—

Knysna.	*Hypothetical.*
Below 8°/oo	Below 5°/oo
8·8 to 21·7°/oo	5 to 15°/oo
Above 28·4°/oo	15 to 25°/oo
Above 34·5°/oo	Above 25°/oo

While we wish to reserve a general discussion of faunistic divisions until we have gathered more evidence from other estuaries, two points must be mentioned here. The first concerns the top of the estuary. Here, either the hypothetical salinity range is too low or the salinity average for Charlesford Rapids is based on too few records to give a fair representation of normal conditions there. Reference to Table II shows that seven estimations of salinity were made for Charlesford Rapids and that two of the samples were taken during a drought.

The second point concerns the mouth of the estuary. In Knysna it has been shown that the channel between the Heads has an average salinity above $34{\cdot}5^\circ/_{\circ\circ}$ and a reduced but typically marine fauna with no estuarine elements. On p. 370 a statement by Krige (1927) was quoted to the effect that Knysna is a drowned valley, *i.e.* the original mouth has been submerged by the sea. In fact, all the evidence of wave action, salinity, and fauna indicates that the channel between the Heads is a sheltered arm of the sea and not really estuarine. Now if this channel does not correspond with the mouth region of an ideal estuary in which estuarine conditions give way to marine ones, we must look for the change higher up.

There is a marked change from clean sand and rock to muddy sand between Fountain Point and Leisure Isle, and there is a corresponding change in the fauna. In this short stretch, thus, is included the mouth region of the ideal estuary. The longer stretch from Leisure Isle to The Point, which has been referred to as the Lagoon, and where the salinity varies from $35{\cdot}7^\circ/_{\circ\circ}$ to $28{\cdot}4^\circ/_{\circ\circ}$, would then correspond to the Middle Reaches. Above The Point is an overlap region extending as far as the upper part of Belvedere, where the substratum and biota of the main channels resemble those of the Middle Reaches and those of the muddy backwaters resemble those of the Upper Reaches. Above Belvedere and as far as the Old Drift (that part referred to as the Westford Channels) conditions are fairly uniform, the salinity varies from $21{\cdot}7^\circ/_{\circ\circ}$ to $8{\cdot}8^\circ/_{\circ\circ}$, and the banks and substratum are mud. This region clearly corresponds to the Upper Reaches.

These conclusions must be regarded as tentative and may need to be modified in the light of further observations.

The importance of a deep permanent mouth is clearly shown by the richness of the Knysna fauna as compared with the poor fauna of Klein River Lake described by Scott, Harrison, and Macnae (1952). In the latter, a marine fauna similar to that of the rocky Knysna Heads could not be expected. But a fauna similar to that of the Knysna Lagoon might reasonably be expected, and it is only represented by a few species such as *Solen capensis*, *Arenicola loveni*, and *Echinocardium cordatum*, which are found on the inside of the sand-bar which usually separates Klein River Lake

from the sea. Another point which has not been brought out here, because we have deliberately omitted a discussion of the fishes, is that the rich fish population of Knysna which mainly migrates from the sea into the estuary and back again is largely absent from Klein River Lake with its shallow and very temporary mouth.

The importance of turbidity can only be appreciated by a comparison of the Knysna fauna with the fauna of other South African estuaries. Knysna has relatively clear water, luxuriant *Zostera* beds extending well below the tide marks, and a rich bottom fauna. Many other South African estuaries are very turbid. The extreme example is the Umzimkulu where a Secchi disc disappears less than an inch below the surface in summer, and it has been found that Secchi-disc readings less than 10 inches are common in most South African estuaries. In these cases the submerged aquatic vegetation is very poor and the bottom fauna very limited indeed.

These points as well as the proportion of tropical and temperate forms in the estuaries round the South African coasts will be discussed again in later papers.

Summary.

The physical conditions and the benthonic fauna of Knysna estuary have been described. It is a clear-water estuary with a deep rocky mouth on the south coast of South Africa. The fauna is very rich. There are four faunistic divisions determined by differences in wave action, salinity, and substratum. These faunistic divisions have been compared with those of an ideal estuary. The distribution and abundance of the different species are summarised in an Appendix.

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Photo: South African Railways.

Aerial photograph of Knysna Estuary and district. In the background are the Outeniqua Mountains, and in the foreground the mouth of the Lagoon opens to the sea between the Heads. On the extreme right are Paarden Island with Thesen's Wharf and Leisure Isle. Across the centre the railway and its bridge are visible.

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APPENDIX

Knysna Estuary Faunistic List.

Comparative abundance of species is indicated by letters in columns under the different stations as follows: P present, F fairly common, C common, LC locally common, A abundant. Species belonging to the various categories given in Table III are indicated by symbols: * indicates "typical seashore species", † indicates "typical estuarine species", ‡ indicates "brack-water species", and ○ indicates pelagic species. In these categories no attempt has been made to classify the smaller animals such as Hydrozoa, amphipods, etc., which were not included in Stephenson's list. Species not yet identified are given their catalogue numbers, *e.g.* Yellow sponge 6T. Owing to the fact that no sponges or ascidians have as yet been identified and it is difficult to determine the number of species present, it was decided to omit these groups entirely from the summary in Table III.

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
PORIFERA										
Blackish, long oscula. 189C	P									
Branching, white. 17C			P							
Fibrous, red. 21N							P			
Grey. 192B		P								
Grey, incrusting. 34B				P						
Grey, irregular. 189D	P									
Greyish-blue, irregular. 192A		P								
Leuconia sp.? 192D		P								
Massive, yellow. 6T	P	P	C	C	F	C	C			
Mauve. 193D		P								
Mauve, crater-like oscula. 18B	P									
Orange, incrusting. 7G				P						
Red, incrusting, Ascidian-like. 7H	P			P			P			
Small, red, prominent oscula. 17F			P							
Small, white, bristly. 192C		P								
Smooth, black, yellow inside. 17E			P							
Smooth, brown, small. 7F				P						
Soft, orange. 17D			P							
Spherical brown. 18D	P									
Tubular stalked, minute. 44A						P				
White, tubular. 17B			P	C	P					
Yellowish, tall oscula, ex 17D		P								
COELENTERATA: HYDROZOA										
Aglaophenia ?dichotoma (M. Sars)			P	C		P				
Bougainvillia ramosa (van Ben.)		P								
Halecium ?tenellum Hincks				P						
Halicornaria arcuata (Lamx.)			P	P						
*Hydractinia ?*sp.				P	P	P				
Kirchenpaueria pinnata (Linn.)	P	P	P	C						
Obelia dichotoma (Linn.)		P								
Plumularia pulchella Bale		P	P							
Plumularia setacea (Ellis and Sol.)				P						
Sertularella arbuscula (Lamx.)			P	P						
Sertularella ?gaudichaudi (Lamx.)	P									
Sertularella ?tumida Warren				P						
Sertularia operculata Linn.	P			C		P				
Syncoryne ?eximia (Allman)		P								
Thecocarpus formosus (Busk)	P		P	P						
Thecocarpus sp. 30R				P						
Thuiaria bidens (Bale)				P						
Tubularia ?betheris Warren	P	P	P							
COELENTERATA: ACTINOZOA										
**Actinia equina* Linn.		P	P							
**Alcyonium fallax* Lutts.	P									
**Anthothoe stimpsoni* (Verr.)	P									

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
COELENTERATA: ACTINOZOA (*Cont.*)										
**Bunodactis reynaudi* (M.-Edw.)	P	P								
Melitores dichotoma Pallas	P									
**Pseudactinia flagellifera* (Hertw.)	P	P	F	C		P				
POLYZOA										
Alcyonidium ?chondroides O'Don. and de Watt.			P	P						
Alcyonidium ?rhomboidale O'Don.			P							
Alysidium parasiticum Busk.	P									
Beania vanhöffeni Kluge.	P	P								
Bicellariella ciliata (Linn.)	P									
Bowerbankia ?pustulosa Ellis and Sol.			C	C	C	C	C			
Cellepora avicularis Hincks	P	P								
Cellepora ?simonensis Busk	P									
Chapperia multifida Busk		P								
Costazia costazii (Sav. and Aud.)	P									
Menipea crispa (Pallas)	P	P								
Menipea marionensis Busk.	P	P				P	P			
Retepora ?tessellata Hincks	P	P								
Retepora ?tubulata Busk	P									
Watersipora cucullata (Busk)	P	P								
Encrusting species. 167C		P								
PLATYHELMINTHES										
**Notoplana ovalis* Bock.	P	P								
Planoceran 115	F	P		P		P				
NEMERTINI										
Crimson. 11R			P	P						
Gorgonorhynchus sp. 33A			P	P						
Red-Brown. 190Q	P									
ANNELIDA: POLYCHAETA										
Aonides oxycephala (Sars)			P							
Arabella iricolor (Montagu)		P	P							
†*Arenicola loveni* Kinberg		P	LC	LC	LC					
Aricia angrapequensis Augener			P	P						
Aricia ?latreilli A. and M.-Edw.			P							
**Audouinia filigera* var. *capensis* (Schmarda)	P	P								
Audouinia tentaculata (Montagu)		P	P	P		P				
Bhawania sp. 177A			P							
Ceratonereis erythraensis Fauvel			F	P	P				F	
Ceratonereis sp. 108A										F
Chaetopterus varieopedatus Renieri	P		P							
Dasychone cingulata Grube		P			P	P				
**Dasychone violacea* Schmarda	P	P								
Diopatra neapolitana Delle Chiaje.			F	P						

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
ANNELIDA: POLYCHAETA (*Cont.*)										
**Dodecaceria fistulicola* Ehlers	P									
Eteone foliosa Quatref.			P							
Eunice aphroditois (Pallas)		P								
Eunice australis Quatref.	P									
Flabelligera affinis Sars	P	P								
Glycera convoluta Kef.			F	F	F	F	P	P		
Glycera prashadi Fauvel	P									
**Gunnarea capensis* (Schmarda)	P									
Harmothoe aequiseta Kinberg			P	P		P	P			
Heteromastus ?filiformis (Clap.)			P							
Hydroides spinosa (Pixell)	F	C								
? *Jasmineira*							C			
Johnstonia clymenoides Quatref.		P				P				
**Lepidonotus clava* var. *semitecta* (Stimp.)	C	C	P			P	P			
Lumbriconereis coccinea Renieri		C								
Lumbriconereis impatiens Clap.		P	P	P	P					
Lysidice collaris Grube	P									
Magelona papillicornis F. Müller			P							
Marphysa sanguinea (Montagu)	P	P	C	A	C	C	A			
Naineris laevigata (Grube)		P								
Nephthys hombergi Aud. and M.-Edw.			F			F				
Nephthys tulearensis Fauvel		P	F		P					
Nereis operta (Stimpson)		P	P							
Nereis succinea (Leuckart)						P				
Nereis willeyi Day	P	C	P	P						
**Nicolea macrobranchia* (Schmarda)	P	P								
Notomastus giganteus Moore		P	F		F	F				
Opisthosyllis brunnea Langerh.						P				
Parathelepus sp. 89F.					P					
Pectinaria koreni Malmg.			P	P						
**Perinereis capensis* (Kinberg)			P	P						
Perinereis falsovariegata Monro		P		P		F				
Perinereis nuntia var. *vallata* Grube			P							
Piromis arenosus Kinberg			P							
**Platynereis dumerilii* (A. and M.-E.)	P	C	P	P	P					
**Polynoe scolopendrina* Sav.	P									
Polynoe sp. 59C		P								
**Pomatoleios crosslandi* Pixell	A	A	P	P	F					
Prionospio ?malmgreni Clap.							P			
**Pseudonereis variegata* (Grube)	F									
**Sabellastarte longa* (Kinberg)	F	F								
? *Salamancina* (tubes only)	P									
Scallisetosus pellucidus (Ehlers)	P		P	P						
Serpula vermicularis Linn.	P	P								
Spirorbis sp.	C									

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
ANNELIDA: POLYCHAETA (*Cont.*)										
Sthenelais boa (Johnston)		P	P		P					
**Terebella pterochaeta* Schmarda	P									
Thelepus plagiostoma Schmarda			P							
Thelepus setosus Quatref.	F	C	P	F	P	P				
ANNELIDA: OLIGOCHAETA										
107								P		
GEPHYREA										
Physcosoma japonicum Grube		P								
Siphonostoma dayi Stephen			P	P						
CRUSTACEA: CIRRIPEDIA										
**Balanus algicola* Pilsbry				P						
**Balanus amphitrite* var. *communis* Darwin	P									
†*Balanus amphitrite* var. *denticulata* Broch		P	C	C	C	P	P			
†*Balanus elizabethae* Barnard		P	P			P	P	C	F	
Balanus tintinnabulum (Linn.)		P								
**Balanus trigonus* Darwin	F	P	P	P						
Balanus sp. 169B	P									
**Chthamalus dentatus* Krauss	C	P	P	P			P			
Chthamalus sp. 194B		P								
**Octomeris angulosa* Sow.	P	P								
**Tetraclita serrata* Darwin	C	P	P		P		P			
CRUSTACEA: AMPHIPODA										
Amaryllis macrophthalma Hasw.	P	P								
Ampithoe africana Barnard		P								
Caprella equilibra Say			P							
Ceradocus rubromaculatus (Stimpson)	P									
‡*Chiltonia capensis* Barnard										P
‡*Corophium triaenonyx* Stebb.		P	P	A				P	P	C
Cymadusa australis (Barnard)			C	P	P	C		C		
Ericthonius braziliensis (Dana)				P						
Eriopisa chilkensis (Dana)						P	P			
‡*Grandidierella lignorum* Barnard										LC
Hyale hirtipalma (Dana)		P								
Hyale maroubrae Stebb.	P	P								
Hyale grandicornis Kröyer	P									
Jassa falcata (Mont.)		P	C	P?						
Lembos hirsutipes Stebb.	P?	P	P	C						
Lysianassa ?ceratina (Wlkr.)		P								
Melita orgasmos Barnard	P									
‡*Melita zeylanica* Stebb.				P				C		C
Orchomenella plicata Schell.	P	P								

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
CRUSTACEA: AMPHIPODA (*Cont.*)										
Paramoera capensis (Dana)	C	P	P	C						
○*Paratyphis* cf. *promontorii* Stebb.			P							
‡*Parorchestia rectipalma* Barnard				C				A	P	P
Podocerus cf. *cristatus* (Thompson)		P								
Stenothoe gallensis Wlkr.		P	P							
Talorchestia ancheidos Barnard					P					
Talorchestia australis Barnard			P			C				
Talorchestia capensis (Dana)		P	C							
Urothoe cf. *pulchella* (Costa)			C							
CRUSTACEA: ISOPODA										
Cirolana cranchii Leach	P									
‡*Cirolana fluviatilis* Stebb.								A	C	C
Cirolana venusticauda Stebb.		P								
Cirolana venusticauda var. *simplex* Barnard	P									
‡*Corallana africana* Barnard								C	P	P
‡*Cyathura carinata* (Kröyer)								P		P
Cymodocella sp. (juv.)	P									
Dynamenella sp. (juv.)	P	P								
Eurydice longicornis (Stüder)			P	P						
Exosphaeroma antikraussi Barnard	P									
Exosphaeroma hylecoetes Barnard	P		C	F	F	P	P	P		
Exosphaeroma kraussii Tat.	P	P								
Janira capensis Barnard	P									
Janiropsis palpalis Barnard				A						
Leptanthura laevigata (Stimp.)				P						
Ligia dilatata Brandt								C		
Ligia natalensis Collinge			C					P		
‡*Paramunna* sp. 102										C
Paridotea ungulata (Pallas)			C	P		P				
Parisocladus stimpsoni (Heller)		P								
Philoscia sp. 146			P							
‡*Pseudosphaeroma barnardi* Monod.									P	A
‡*Sphaeroma terebrans* Bate									P	F
Stenetrium zyzygus Barnard	P									
Tylos granulatus Krauss		P								
CRUSTACEA: TANAIDACEA										
Leptochelia sp. 139F				A						
‡*Tanais philetaerus* Stebb.										C
CRUSTACEA: CUMACEA										
157D			P							
CRUSTACEA: MYSIDACEA										
○*Gastrosaccus* sp. 157C			P							
○*Leptomysis tattersalli* O. Tat.			P							

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
CRUSTACEA: MYSIDACEA (*Cont.*)										
⊙*Mesopodopsis africanis* O. Tat.			P							
⊙*Rhophalophthalmus egregius* Hans.							P			
⊙124								P		
CRUSTACEA: DECAPODA										
**Alpheus crassimanus* Heller . .			F	C	C	F	C			
Athanas ?nitescens Leach . .				P						
†*Callianassa kraussi* Stebb. . .		P	P		C		F		C	P
†*Cleistostoma algoense* Barnard .				P						
†*Cleistostoma edwardsii* McLeay .		P	C	A	C	A	A	F		
**Cyclograpsus punctatus* M.-Edw. .	C	C	C	F	C		F	P		
**Dehaanius dentatus* (M.-Edw.) .				P						
Diogenes brevirostris Stimpson .	P	F	A	A	C	F	P			
Diogenes extricatus Stebb. . .								P		
Eupagurus placens Stebb. . .			P							
Hippolyte ?kraussiana (Stimps.) .			P	P	P	F	P			
†*Hymenosoma orbiculare* Decm. .	P	F	C	C	C	C	F	F	P	P
Leander pacificus Stimpson . .	P	P	C	C	P	C	P	C	C	
Macropodia rostrata (Linn.) . .				P						
**Ocypode* sp. 64A . . .				P						
⊙*Penaeus indicus* M.-Edw. . .										P
⊙*Penaeus japonicus* Bate . .		P	P	P						
Pilumnus pisifer (McLeay) . .						P				
**Plagusia chabrus* (Linn.) . .	P									
Porcellana streptocheles Stimpson .		P	P	P						
Processa ?edulis				P						
†*Scylla serrata* (Forskal) . .			P				C	P		
†*Sesarma catenata* (Ortm.) . .			C	C	C	A	A	F		
Thalamita ?admete (Herbst) . .				P						
†*Upogebia africana* (Ortm.) . .		P	A	A	A	C	F	P		
CRUSTACEA: STOMATOPODA										
Squilla ?armata M.-Edw. . .			P							
ARACHNIDA: PYCNOGONIDA										
Nymphon setimanus Barnard .				P						
173		P	P							
ARACHNIDA: ARANEIDA										
Desis tubicola (Pocock) . .	P									
INSECTA										
‡*Argyrobothrus* sp. 106C . .										P
‡*Clypeodytes* sp. 159C . .										C
‡*Ischnura* sp. 184E . . .										P
‡*Leptocerrus* sp. 106 . . .										P
‡*Leptocerrus* sp. 159A . . .										A
‡*Sigara contortuplicata* (Kirk) .										P

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
MOLLUSCA: AMPHINEURA										
**Acanthochiton garnoti* (Blainv.)	C	P	P	P	P	P	P			
**Chiton tulipa* Q. and G.	F									
**Dinoplax gigas* (Gmelin)	P									
**Ischnochiton tigrinus* (Krauss)	P									
Ischnochiton sp. 6R	P	P	P	P	P	P				
Scaly-mantled chiton. 38C.					P		P			
MOLLUSCA: PELECYPODA										
? *Anomia* 6S			P	F						
**Barbatia obliquata* (Wood)	P	P								
Cardium sp. 11P			P	F						
Chlamys sp. 141C	P	P		P						
Cytherea hebraea Sow.			P	P						
Dark brown. 89A					P					
Heavy, rounded. 36D						P	P			
Lima rotundata Sow.	P	P	P	F						
†*Loripes clausus* Phil.		P	F	F	F	F	F			
Lyrodus sp. 45A						P				
†*Modiola capensis* Krauss				F	F	F	C	A	A	P
Mottled triangular. 61C								P		
**Mytilus perna* (Linn.)	A	P		P						
Ostrea algoensis Sow.	P									
**Ostrea margaritacea* Lam.	C	A	P	F	P	P	P			
**Pinctada capensis* (Sow.)			P							
Pinna squamifera Sow.		P	P	P						
Radiating bands on shell. 89B					P					
Saxicava sp. 189M	P									
†*Solen capensis* Fischer					F	F	C			
? *Tellina* 36C					P	P	P	P		
Teredo navalis Linn.						P				
**Thecalia* ?*concamerata* (Brug.)	P	P								
Tivela compressa Sow.			P							
Tivela sp. 19B		P								
Venus ?*verrucosa* (Linn.)				P						
White, very inequilateral. 89C					P					
MOLLUSCA: GASTROPODA										
Aplysia sp. 20A	P	P								
? *Assiminea* 31A			P	P	C	C	P	C	P	
Berthella granulata (Krauss)	P									
Bullia annulata Lam.	P	P	P							
†*Bursatella leachii* var. *africana* Engel		P	C	C	P	F	F			
Calliostoma africanum Bartsch		P								
Cassis achatina Lam.			P							
**Cominella cincta* (Röding)	C	P	P	P	P					
**Cominella elongata* (Dunker)	P	P								

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
MOLLUSCA: GASTROPODA (*Cont.*)										
**Crepidula hepatica* Deshayes .			P		P					
**Diodora ?mutabilis* (Sow.) . .	P	P	P	P						
Doris sp. 18L	P									
Doris sp. 46A				P						
Drillia sp. 6Q	P	P	P	P						
? *Eolis* 28A			P							
Gibbula sp. 60	P	P	F	F						
**Gyrina pustulata* (Euthyme) .	P									
**Haliotis midae* Linn. . . .	P									
†*Haminea alfredensis* Bartsch .			C	C	C		P		P	
**Helcion pectunculus* (Gmelin) .	C	C	P							
**Helcion pruinosa* (Krauss) . .	P	P	P							
**Littorina ?africana* Philippi . .						P				
**Littorina knysnaensis* Philippi .	A	A	A	A	C	C	C	C	P	
? *Littorina* 31C . . .				P		P		P		
Lotorium olearium Deshayes .			P							
†*Nassarius kraussianus* (Dunker) .			C	C	C	C	C			
Nassarius ?plicosus . . .				P						
†*Natica imperforata* Gray . .		F	C	C	P	P	P			
**Nerita albicilla* Linn. . . .					F					
**Oxystele sinensis* (Gmelin) . .	C	P								
**Oxystele tigrina* (Dillwyn) . .	C	C	P							
**Oxystele variegata* (Anton) . .	A	F	P		C		C			
**Patella argenvillei* Krauss . .	F									
**Patella barbara* Linn. . . .	F									
**Patella cochlear* Born . . .	A									
**Patella granularis* Linn. . .	C	P								
**Patella longicosta* Lam. . .	F									
**Patella miniata* Born . . .	P	P								
**Patella oculus* Born . . .	C	F	P		P					
Philine aperta Lam. . . .			P							
Rissoa pinna			C	C	P	C			P	
**Siphonaria ?aspera* Krauss . .	C	C	F	F	F	P	F			
**Siphonaria capensis* Q. and G. .	P			F	P	P		P		
**Siphonaria deflexa* Heldling . .		P								
**Siphonaria oculus* Krauss . .	P		P	P	P	P				
Small smooth whelk. 185E .		P								
Small striped *?Gibbula* 192H .		P								
**Thais dubia* Krauss . . .	P	P	F	P	P		P			
Tornatina meridionalis Smith .	P									
Tricolia sp. 168D . . .		P								
Tricolia sp. 189R . . .	P									
**Turbo cidaris* Gmelin . . .	P			P						
**Turbo sarmaticus* Linn. . .	P	P								
Turritella carinifera Lam. . .				P						
†*Turritella knysnaensis* Krauss .		P	C	C	C	F				

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
MOLLUSCA: CEPHALOPODA										
Octopus vulgaris Lam.		P	P	P						
○*Sepia officinalis* L.			P	P						
○*Sepia* sp. 189A	P									
ECHINODERMATA										
Amphipholis squamata (D. Chiaje)				P						
**Asterina exigua* (Lam.)	C	P	F	P	F		P			
Astrocladus euryale (Retzius)	P									
Astropecten antares Döderlein			P	P						
Astropecten sp. 16A			P							
Black Holothurian. 189F	P									
**Cucumaria frauenfeldi* Ludwig	P									
Echinocardium cordatum (Penn.)			F							
Echinodiscus bisperforatus (Leske)			P							
Epitomapta knysnaensis Cherb.		P	P	P	P	P				
**Henricia ornata* (Perrier)	P	P								
**Marthasterias glacialis* (Linn.)	F									
**Ophiothrix triglochis* M. and Tr.	P			P	P	P				
**Parechinus angulosus* var. *pallidus*	C	P	C	C		F				
**Patiria bellula* Sladen	P									
Red Holothurian. 189G	P									
TUNICATA										
Ascidia sp. 20F	P	P								
Black irregular compound. 185A		P								
Fawn Didemnid. 169E	P									
Flat, grey, leaf-like. 32C				P						
Pyura stolonifera (Heller)	C	P	P	C	F	F	P			
Reddish meandering compound. 185B		P								
Sand-covered simple. 7E				P						
Stalked simple. 189H	P	P								
Tough reddish compound. 169F.	P	P								
White Didemnid. 6U				P			P			
ALGAE: CHLOROPHYCEAE										
Bryopsis sp. 66B				LC						
Codium tenue Kuntz. 23A					P	LC	P			
Enteromorpha sp. 68C		C	C							
Ulva lactuca Linn.	P	P								
Ulva sp. 66A			C	C	C	C				
ALGAE: RHODOPHYCEAE										
Bostrychia scorpioides (G.M.) Moss			LC							
Gelidium pristoides (Turn.) Kütz.	A	C								
Gelidium sp. 195J								P		
Laurencia sp. 66C				P						
Plocamium sp. 35A			F							

Species.	Station.									
	Fountain Point.	Woodbourne.	Leisure Isle.	Brenton and Paarden Island.	Rail Bridge.	The Point.	Belvedere and Eastford.	Westford Bridge.	Old Drift.	Charlesford Rapids.
ALGAE: RHODOPHYCEAE (*Contd.*)										
Polysiphonia incompta Harv.				P						
Tayloriella tenebrosa (Harv.) Kylin			P							
Zonaria tournefortii (Lamour) Mont.			F	C						
FLOWERING OF PLANTS										
Arthrocnemum africanum Moss.			P							
Chenolea diffusa Thg.			C	C	C	C	F	LC		
Cotula coronopifolia Linn.							F	C	F	A
Felicia ficoidea D.C.			P							
Halophila ovalis			LC	LC		F	P			
Juncus kraussii Hochst.			P	LC	LC	LC	A	A	F	
Limonium linifolium O. Kuntz.		C								
Phragmites communis							P	P	P	P
Puccinellia fasciculata (Torr.) Bickn.			P	A	A	A	A			
Ruppia sp. 150								P	F	C
Salicornia meyeriana Moss.			A	LC	A	A	A	LA	P	
Scirpus globiceps C. B. Clark										LA
Scirpus venustulus (Kunth) Boeck										C
Spartina stricta Rotm.							P			
Spergularia marginata (D.C.) Kitt.			P							
Triglochin elongatum Bucher			A		C	C			C	C
Zostera capensis Setchell			A	A	A	A	A	LA	F	

OBSERVATIONS AND EXPERIMENTS ON FOULING ORGANISMS IN TABLE BAY HARBOUR, SOUTH AFRICA.

By Naomi Millard, Ph.D., Department of Zoology, University of Cape Town.

(With Plates XXXII and XXXIII and seven Text-figures.)

(Read March 21, 1951.)

CONTENTS.

Introduction.

This research was instigated by a request from the Marine Corrosion Sub-Committee of the Iron and Steel Institute, London, for information on the fouling organisms found on the hulls of ships which were dry-docked in Table Bay. Later, the somewhat fragmentary knowledge obtained by the examination of ships' hulls was supplemented by the regular observation of experimental plates immersed in Table Bay Harbour. In its final form the research had two distinct objectives: (*a*) Investigation of marine fouling in South Africa. Studies of marine fouling made in Great Britain, America, Hawaii and Australia will be discussed at the end of this paper, but this is the first investigation of its kind in South Africa. (*b*) Investigation of the settlement and rates of growth of this particular group of infratidal organisms, which appears to occupy its own ecological niche. This supplements

and extends earlier observations of the same type on intertidal organisms by Millard (*née* Bokenham) and Stephenson (1938).

The author wishes to thank the following for their kind co-operation during the course of the work: Commander W. J. Copenhagen of the S.A.N.F. and the staff of H.M.S.A.S. "Unitie", the docking authorities of Table Bay Docks, the Royal Cape Yacht Club, the Table Bay Power Station, Mr. K. A. Pyefinch of the Marine Station, Millport, the Chemistry Department of the University of Cape Town, and the specialists responsible for the identification of material. Among the latter are Dr. G. Ranson of the Musée Nationale d'Histoire Naturelle, Paris (Oysters); Miss R. D. Turner of the Museum of Comparative Zoology, Cambridge, Massachusetts (Teredinidae); Dr. K. H. Barnard of the South African Museum (Isopods and Amphipods); Dr. H. G. Stubbings, Central Metallurgical Laboratory, Emsworth (Barnacles); Professor J. H. Day, Dr. K. M. F. Scott and Miss P. Smuts, all of the University of Cape Town (Polychaets, Polyzoa and Algae). The expenses connected with the work were defrayed by a grant of £30 from the Staff Research Fund of the University of Cape Town.

The observations on which this paper is based were conducted over a period of over three years, namely from March 1946 to January 1950, and fall naturally into two categories:

A. Direct observations of the fouling growths on ships' hulls when brought into dry dock. These examinations were performed at irregular intervals throughout the above-mentioned period. They provided valuable information on the range and variety of fouling organisms, but gave only scanty information on rates of growth, seasons of settlement, etc. Moreover, except where it was known that the vessel had not left the Cape Town area, it was not possible to differentiate definitely between exotic and endemic forms.

B. Regular examination of experimental plates. These observations had several advantages. The organisms concerned could be considered as local forms, although the possibility of some of them being immigrants was always borne in mind. The date of settlement could be determined within narrow limits, and thus the rate of growth and the succession in the fouling community could be worked out. The arrangement of plates at different levels and the coating of one series with an anti-fouling paint would provide information on zonation and the effect of anti-fouling paints in South Africa. Lastly, the settlement on the stationary plates could be compared with that on a moving ship.

It was originally intended to include a complete list of fouling organisms as an appendix, but owing to the fact that many of the identifications have not yet been received from the specialists it was decided to publish the paper as it stands and to postpone the final list of organisms to a later date.

Description of Apparatus and Method of Work.

The experimental plates were all 7 × 3 in. (17·8 × 7·6 cm.) in size, drilled at the four corners for attachment to a frame. This size was convenient, because each plate could be detached and carried to the laboratory in a large jar of sea-water, where it was examined under water in a shallow dish with the aid of a dissecting microscope. The plates were of ⅛ in. black steel. Before using they were pickled in commercial hydrochloric acid and scrubbed with a wire brush to remove mill-scale, washed and then painted with two coats of a standard anti-corrosive paint.

Two frames were constructed as shown in Plate XXXII, fig. 3. Each consisted of 4 uprights of angle iron 4½ ft. in length, attached top and bottom to circular discs 15½ in. in diameter. The uprights were drilled with holes at 3-inch intervals for the attachment of the plates. These frames were treated in a similar manner to the plates. The plates were attached to the uprights in a horizontal series by means of zinc-coated wire which could easily be cut for removal.

The frames were suspended from the quay outside H.M.S.A.S. "Unitie" in Table Bay Docks, with the bottom of each 2 ft. 11 in. above the mud-line, and the top about 5 ft. 9 in. below Low Water Springs. For examination the whole frame was hauled up and the required plates detached.

For experiments on zonation an ex-navy crate-type raft was moored in the harbour of the Royal Cape Yacht Club in about 16½ ft. of water (Low Water Springs). The same plates were used, and were suspended at different levels from the side (Plate XXXIII, fig. 2). The salinity of the yachting harbour was 34·9 °/₀₀ on 2/12/48, and there is no reason to expect any major fluctuation throughout the year, or any appreciable difference between the yachting harbour itself and the quay outside "Unitie".

Estimates of the fouling were made in the laboratory (*a*) by counting the number of macroscopic organisms, and (*b*) by weighing. It was found that for short periods of observation the first method was more useful, but over longer periods, when the main change in the organisms was one of growth, the second method was more significant. When the number of organisms was not too large, actual counts were made, but when very numerous, those on a typical square inch were counted and an average obtained for the plate.

The second of these methods was unavoidably subject to many inaccuracies, and any weights submitted in this paper are thus approximate only. It was felt that in the estimation of a fouling component any water held within the bodies of the organisms forms an essential part of that component, hence it is the *wet* weight which is important and not the dry. Consequently it is the wet weight which has been used. All plates were

treated in a similar manner, each being removed from a jar of sea-water, allowed to drain for 10 seconds and then weighed in a beaker.

Seasonal Settlement.

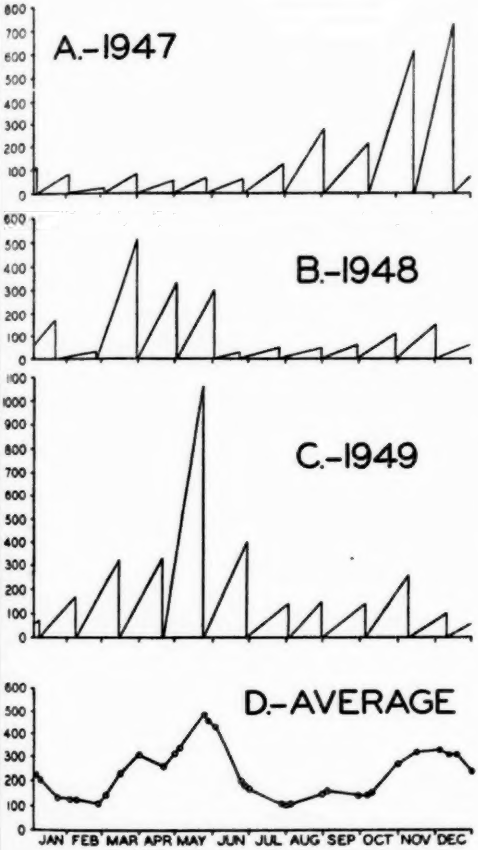
The seasonal variation in the fouling component was determined by immersing a series of plates for 4–5 weeks each throughout a period of three years, 1947, 1948 and 1949. This will be called *Series I*. The results are shown in text-figs. 1 and 2.

Text-fig. 1 illustrates the fouling record as shown by weight, and text-fig. 2 as shown by numbers. In each case the fourth diagram (D) is in the form of a graph illustrating the average fouling over the three years. In text-fig. 2 the barnacle component of the fouling is indicated in solid black. In this figure the number of organisms for the first three records in 1947 was based on estimations only and so is shown in dotted lines. In both text-figures the third record (February) in 1947 is probably lower than it should be, because the frame became detached during the period and fell to the bottom. The numerical record in text-fig. 2 has not included several settlements of *Mytilus*, due to the difficulty of making counts of the numerous specimens present amongst and within the shells of the barnacles. These settlements are indicated in text-fig. 3, and since they occurred chiefly during the months of February to March, and to a lesser extent during November to December, would cause a rise in the graph in text-fig. 2 D, during these periods, but would not alter its configuration to any appreciable extent.

The data must thus be regarded with reservations. When considered as a whole, the point that first strikes the eye is that there are two peaks in the fouling intensity during the year, one in autumn, extending roughly from March to May, and another in spring from September to December. The fact that these peaks are due almost entirely to the barnacle component is well illustrated in text-fig. 2 and will be discussed again later.

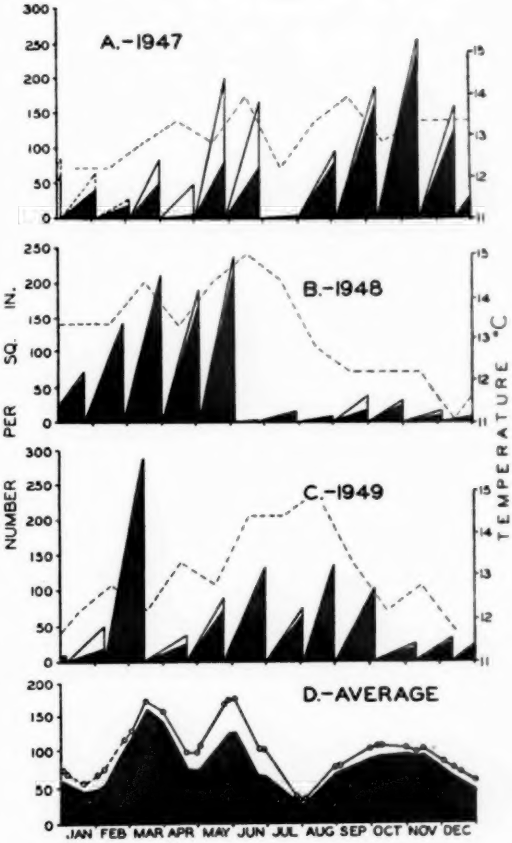
Another point illustrated by text-fig. 2 for the years 1947 and 1948 is a distinct falling off in the settlement during the winter months June to August. This "off season" is probably due largely to weather conditions and certainly varies considerably from year to year. It started earlier in 1948 than in 1947 and was of longer duration. In 1949 there was no falling off in the *number* of organisms which settled during the winter, but their growth-rate was not on a par with that of the earlier months of autumn, as can be seen in text-fig. 1 C.

The seasons of settlement of individual organisms during the three-year period are illustrated in text-fig. 3. An attempt has been made to indicate the periods of maximum abundance by thickenings of the lines, although



TEXT-FIG. 1.—Diagram illustrating the seasonal fouling [illegible]cord over a three-year period in Table Bay, as shown by [illegible]ight. Records from experiments, Series I.

In this and the following diagram the fouling for each 4 [illegible] 5 weekly period is represented by a figure starting from [illegible] when a plate was immersed and increasing to a maximum when it was removed.



TEXT-FIG. 2.—Diagram illustrating the seasonal fouling record over a three-year period in Table Bay, as shown by numbers. Records from experiments, Series I. The solid black represents the barnacle component of this fouling. In A, B and C the mean monthly temperatures are shown by broken lines.

the numbers of the different species are in no way comparable with one another. The greatest thickening represents the largest number of that particular organism to occur during the period. The record cannot be considered complete, since many small settlements may have missed the plates altogether, but it does at least give an indication of when the larval stages can be expected to be present.

Several hydroids have occurred on the plates, of which the most important from the fouling point of view are *Tubularia crocea* (L. Agass.) and *Kirchenpaueria pinnata* (Linn.). Both often occur in thick carpets on the hulls of ships. *Tubularia* settled mostly in the spring and summer. On ships' hulls it may be present at any time of the year. *Kirhcenpaueria* had its period of maximum settlement in spring, and *Obelia dichotoma* (Linn.), which was also fairly common, settled almost entirely in the autumn. Three other species of hydroids occurred more rarely, namely *Obelia geniculata* (Linn.), *Plumularia setacea* (Ellis and Sol.) and *Gonothyraea loveni* (Allman), which have not been represented in text-fig. 3.

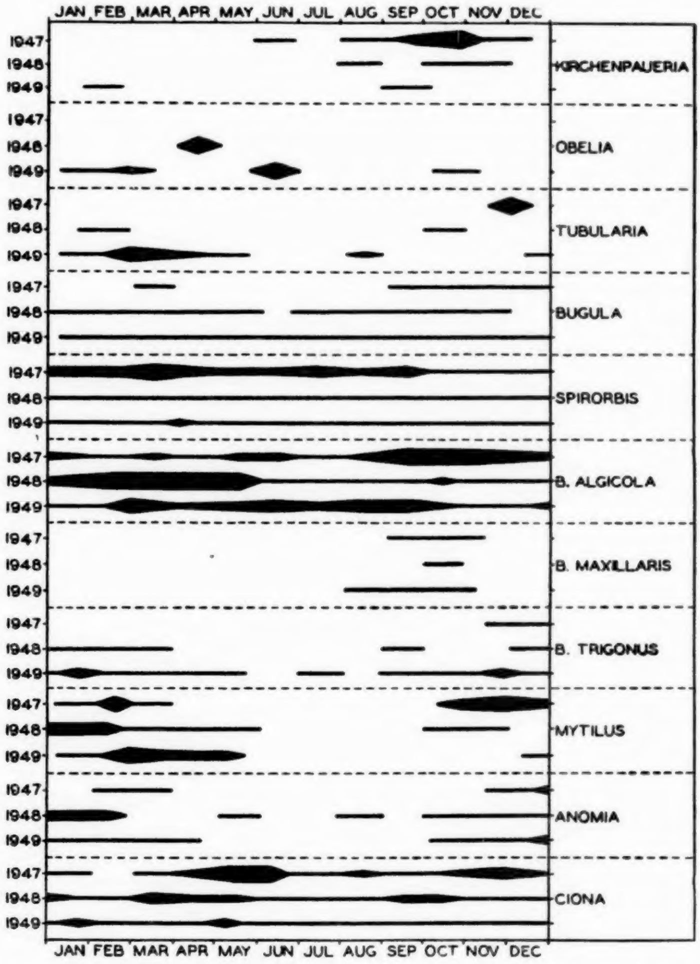
The polyzoan *Bugula calathus* Norman, and the tube-worm *Spirorbis borealis* Daud., settled at all times of the year. The latter was present in great numbers during 1947, and showed indications of a season of maximum abundance in autumn.

Three species of barnacles settled during the experiments, namely *Balanus algicola* Pilsbry, *B. maxillaris* Gronovius and *B. trigonus* Darwin, all of which also occur in the lower parts of the intertidal zone along the shore. Of these, *B. algicola* was easily the most common, and accounted for practically the whole of the barnacle component in text-fig. 2. It settled in every month of the year, but showed two periods of maximum abundance, one in spring from September to December, and one in autumn from March to June. It has already been suggested in a previous paper (Bokenham and Stephenson, 1938) that this barnacle has two breeding seasons during the year. The other two species occurred in smaller numbers, *B. maxillaris* settling only in spring, and *B. trigonus* sporadically throughout the year, though most numerous in late summer.

Mytilus settled from October to May, most abundantly in November–December and in February–March. It was not possible to establish with certainty the species of the mussels at this early age, but it is suspected that most of them were *M. meridionalis* Krauss with possibly a few *M. crenatus* Lamarck. *Anomia* settled in small quantities at irregular intervals throughout the year.

The sea-squirt *Ciona* was one of the most important fouling organisms, ranking second only to the barnacles. It settled throughout the year, with a season of maximum abundance during the autumn months March–June, and a less marked one during the spring from September to December.

As in Great Britain (Pyefinch, 1946), so in South Africa, there is a tendency for the fouling to vary from year to year. This is illustrated by the



TEXT-FIG. 3.—Diagram illustrating the seasonal settlement of the more important fouling organisms in Table Bay during the years 1947–49. Records from experiments, Series I.

records for the years 1947 to 1949. Speaking generally, the fouling was heavy during the latter half of 1947 and the first half of 1948 and 1949.

This was due chiefly to *Balanus algicola*, but also involved the hydroids and mussels.

Finally, it is obvious that the very marked seasonal variation in the fouling, as encountered for instance in Great Britain, is much less marked in South Africa. It has been stated by the Marine Corrosion Sub-Committee of the Iron and Steel Institute, London (1944), that "in some tropical ports . . . extensive fouling will occur nearly all the year round".

The Relation between Water Temperature and the Seasonal Record.

Temperature records for the period under observation were obtained by courtesy of the Table Bay Power Station. These are quoted in Table I, and represent monthly averages obtained from half-hourly readings taken from the Power Station intake. This intake opens inside the

Table I.—Mean Monthly Temperatures in °C. over the Period 1946–1949.

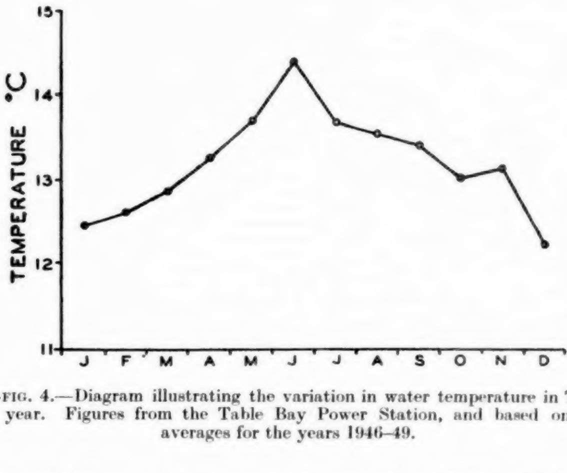
	1946.	1947.	1948.	1949.	Monthly Average.
January . .	12·2	12·2	13·3	12·2	12·5
February . .	12·2	12·2	13·3	12·8	12·6
March . .	12·2	12·8	14·4	12·2	12·9
April . .	13·3	13·3	13·3	13·3	13·3
May . .	15·0	12·8	14·4	12·8	13·8
June . .	14·4	13·9	15·0	14·4	14·4
July . .	13·9	12·2	14·4	14·4	13·7
August . .	13·3	13·3	12·8	15·0	13·6
September .	14·4	13·9	12·2	13·3	13·5
October . .	15·0	12·8	12·2	12·2	13·1
November. .	14·4	13·3	12·2	12·8	13·2
December . .	12·8	13·3	11·1	11·7	12·2
Yearly Average .	13·6	13·0	13·2	13·1	13·2

Duncan Dock (and in the same basin where the experiments were performed) at a depth of about 30 ft. below sea-level, and runs by an underground culvert to the Power Station, where the temperatures are taken before the water enters the condensers. Due to the immense volume of water continually passing through the pipes (approx. 10 million gal. per

hour), the change in temperature between the dock itself and the storage tank can be regarded as negligible.

The temperature records for the years 1947, 1948 and 1949 are plotted on text-fig. 2, together with the fouling records for those years. The mean monthly record for the total period 1946–1949 is illustrated in text-fig. 4 and needs some explanation.

It is a recognised fact that the water temperatures along the west coast of South Africa are considerably lower than those along the south and east coasts. These low temperatures are due to the upwelling of a cold



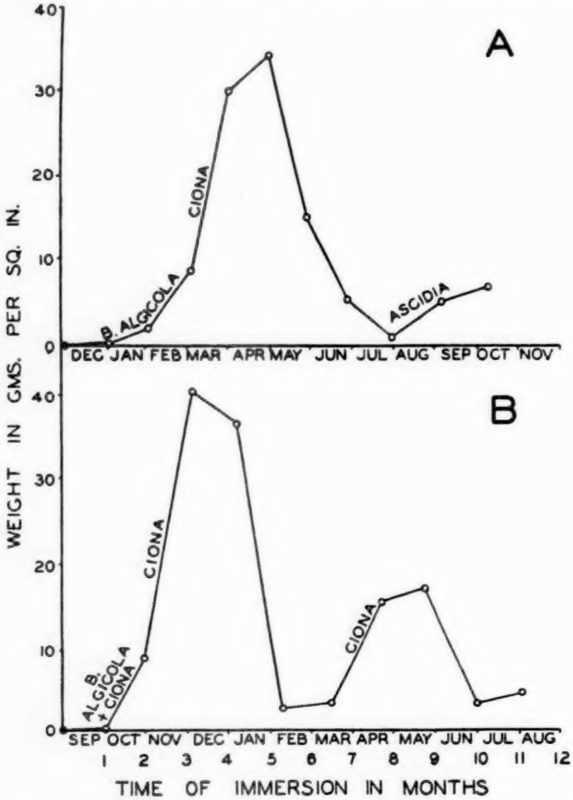
TEXT-FIG. 4.—Diagram illustrating the variation in water temperature in Table Bay over the year. Figures from the Table Bay Power Station, and based on monthly averages for the years 1946–49.

body of water known as the Antarctic Intermediate Water, which becomes incorporated in the northward-flowing Benguela current. The amount of upwelling is influenced considerably by the direction of the prevailing wind. As shown in text-fig. 4, low-water temperatures (below 13° C.) occur in Table Bay during the summer months December–March, at which time the prevailing south-easterly winds tend to drive the surface waters away from the coast and so enhance the upwelling effect. Maximum water temperatures occur during the winter months May, June and July, when the prevailing north-westerly gales tend to drive the warmer surface waters towards the coast and so reduce the upwelling effect.

It must be noted here that Isaac (1937) has given temperature records for selected stations on the South African coast, one of which was the old Cape Town Pier, which has now been demolished in the construction of the new Duncan Dock. If Isaac's graph is compared with the one produced here, its curve will be seen to be exactly the opposite, namely, with minimum

temperatures from June to October and maximum ones in December and January.

The difference possibly arises from the fact that Isaac's records were surface temperatures, taken during daylight hours only and thus con-



TEXT-FIG. 5.—Diagrams illustrating the accumulative fouling record in Table Bay, as shown by weight.

A. Experiment, Series II, commencing 3/12/46, and continued for $10\frac{1}{2}$ months.

B. Experiment, Series III, commencing 30/8/48, and continued for 11 months.

siderably influenced by convection from the air. His monthly averages were based on records taken twice a day (personal correspondence). The validity of the Power Station records can hardly be questioned, since each monthly average is based on approximately 1440 readings. Moreover, Mr. Clowes of the Division of Fisheries has kindly allowed the author to

see the records taken by the Government research vessel off the west coast of the Cape during the last few years. These support the contention that at inshore stations sea temperatures are higher in winter than in summer. It is possible, of course, that the temperature records quoted here are slightly different from those in Table Bay itself. The water within the docks, for instance, might be slightly warmed by the effluent from the Power Station, the temperature of which is a maximum of 10° C. higher than the intake water.

The main fact that emerges from these records is that the temperature range in Table Bay is small, with a monthly average varying from 11·1 to 15·0° C. within a period of 4 years. The effect of a small temperature range on the total fouling record as compared with other parts of the world will be discussed again later. Higher water temperatures in winter might be expected to favour continuous fouling throughout the year and to eliminate a winter "off season". However, it must be borne in mind that in winter the higher water temperatures occur together with violent north-westerly gales and heavy seas, so that in general an "off season" does occur, although, as already remarked, it was not evident in 1949.

Apart from this winter "off season", if the temperature records for the individual years be compared with the fouling records for the same years (text-fig. 2), a certain correspondence can sometimes, though not always, be traced. This is particularly evident in 1949, where a rise in the fouling intensity seems roughly to follow a rise in the water temperature.

Considering the results as a whole, it is suggested that the spring increase in fouling corresponds with the breeding seasons of the more important organisms, which in turn are stimulated by an increase in the light intensity and possibly other factors, but not by an increase in water temperature. On the other hand, the autumn fouling peak may be influenced by an increase in water temperature at this time, and by the fact that some of the spring settlements (e.g. *Balanus algicola*) have now reached maturity and are themselves able to produce young.

The Accumulation of the Fouling and its Succession.

The accumulation of the fouling over a longer period of time was tested by two series of experiments beginning at different times of the year, the first (*Series II*) on 3/12/46, and the second (*Series III*) on 30/8/48. In each case a set of plates was immersed at the starting date, and thereafter individual plates were removed after increasing lengths of time, the first after one month, the second after two, and so on.

The results of these experiments are expressed graphically in text-fig. 5. In Series II (text-fig. 5 A) there was an interval of about a month with

practically no increase in weight, a slow increase for the next month, then a rapid increase, reaching its peak about 5 months after the beginning of the experiment, followed by an equally rapid falling off in weight for 3 months, after which the weight started to increase once more at a slower rate.

During the early part of this experiment the increase in weight was due chiefly to two organisms, the barnacle *Balanus algicola* and the sea-squirt *Ciona*. The young barnacles settled in large numbers (about 58 to the square inch) during the first month of the experiment, and some reached their normal adult size of about 8 mm. in diameter by the beginning of the third month, at which time they were the dominant organisms (Plate XXXII, figs. 1 and 2). Young specimens of *Ciona* were settling during the 2nd and 3rd months, after which time they grew rapidly, reaching their maximum length of 15 cm. by the end of the 5th month, causing the sharp rise in the curve during this period. These organisms settled only on the under sides of the plates, and hung down in dense masses, replacing the barnacles in dominance from the 3rd month onwards (*cf.* Plate XXXII, fig. 4). All the barnacles on the under sides of the plates died off, and many of those on the upper, although a definite barnacle component of the population was kept up by sporadic new settlements of *B. algicola* and persisting small numbers of the slow-growing types such as *B. maxillaris* and *B. trigonus*. The two latter species were still healthy and active at the termination of the experiment after 10 months.

The period of *Ciona* dominance ended in the 6th month, when the animals began to fall off the plates, apparently by sheer weight of numbers, but more probably because they had reached the end of their normal life-span. By the 8th month none of the first generation was left, and from this time on a new type of community became evident. This included a mixed population, of which *Ascidia* sp. was the dominant organism, together with large numbers of hydroids (chiefly *Kirchenpaueria pinnata*, but also *Obelia dichotoma* and *Gonothyraea loveni*) growing on and amongst them. Barnacles were present in fair numbers, including the three species mentioned above, and there were smaller quantities of other organisms, such as the mussel *Mytilus crenatus*, several compound ascidians, the polyzoan *Bugula calathus*, and the tube-worms *Hydroides norvegica* (Gunn.) and *Spirorbis borealis*.

Although of no significance in the general story of the fouling, it might be noted here that there were large settlements of the mussel *Mytilus meridionalis* from the 3rd to the 5th months. These, together with large numbers of diatoms, formed a layer about $\frac{1}{16}$ in. thick on the upper sides of the plates both in and amongst the empty barnacle shells. It was not a successful colonisation, since none reached a length of more than 5 mm. and all had disappeared by the end of July.

The next series of experiments (Series III), starting 30/8/48 and illustrated in text-fig. 5 B, showed a similar sequence of events, though modified by the different season of the year when the experiments began. Here, too, there was a phase of dominance by *Balanus algicola* for the first two months, but this dominance was shared even at this early period by *Ciona* on the under surfaces of the plates, probably due to the fact that the beginning of the experiment coincided with the start of the spring settlement of *Ciona*, whereas the previous experiment (Series II) started in December, *i.e.* half-way between the major spring and autumn settlements. From the 3rd month on *Ciona* assumed complete dominance, and *B. algicola* began to die off as before. This earlier colonisation by *Ciona* had an effect on the whole course of the experiment. As shown in text-fig. 5 B, the peak of *Ciona* dominance was reached sooner, at the end of the 3rd month, and the specimens died and fell off at an earlier stage.

Once the *Ciona* had disappeared, the slower-growing barnacles *B. maxillaris* and *B. trigonus* had a brief period of dominance during the 6th and early part of the 7th months. On the upper sides of the plates these barnacles were seated amongst a rich colony of polychaet worms, whose muddy tubes entirely covered the remaining surface. This worm community persisted throughout the experiment. The dominant species were *Polydora* sp. and *Scolecolepis* sp. Such communities have also been observed in other similar situations in the dock area, and in general contain a variety of additional species, including *Polydora flava* Clap. (common), *P. hoplura*? (common), *Capitella capitata* (Fabr.) (common), *Nereis caudata* (Delle Chiaje), *Syllis brachychaeta* Schm., *Lumbriconereis tetraura* (Schm.), *Parapionosyllis* sp., *Cirratulus chrysoderma* Clap., *Platynereis dumerilii* (A. & M. E.), *Nicolea macrobranchia* (Schm.) and *Audouinia tentaculata* (Mont.).

Towards the end of the 7th month a new colony of *Ciona* settled on the lower sides of the plates and rapidly assumed dominance, causing a second peak in the fouling intensity at the end of the 9th month. This settlement coincided with the period of autumn settlement and occurred during March. The sequence of events was thus repeated, and by the 11th month this second colony of *Ciona* had disappeared, and the plates were left with a mixed population of barnacles (*Balanus algicola*, *B. trigonus* and *B. maxillaris*), polychaet worms (mostly *Polydora* sp.), encrusting polyzoa (*Lepralia* ? *pallianassa*), and a few mussels (*Mytilus meridionalis*, *M. crenatus*, and a small white species).

An attempt will now be made to discuss these results in relation to South African waters in general and with reference to observations on ships' hulls.

The importance of a primary film of microscopic organisms in laying a

foundation for the attachment of larger forms has been stressed by numerous workers. Thus, Zobell (1935) has emphasised the importance of bacteria in this connexion, Wood (1950), algal spores and diatoms, and Wilson (1925) and Scheer (1945), diatoms. Scheer found that an early settlement of diatoms favoured the development of a Bryozoan community in California, but did not appreciably affect other communities.

A study of microscopic organisms was beyond the scope of this work, but scattered observations suggest that although diatoms and bacteria are generally present during the first month of exposure and sometimes in considerable numbers, they are not essential for the settlement of other forms, as for instance barnacles. When present they usually occur together with a colonial ciliate, probably *Zoothamnion*, which has previously been recorded by Bishop (1946) as an important fouling organism in estuarine or polluted conditions in Great Britain, and also by Scheer (1945) from California and Allen and Wood (1950) from Australia.

The early success and dominance of the fast-growing *Balanus algicola* seems to be a typical feature of South African waters and has been noted on many occasions. This species appears to be normally shortlived: it grows rapidly, reaches maturity in about 2 months, and dies off within 7 months. (Compare also Bokenham and Stephenson, 1938.) In the present experiments, the barnacles lived for only 3–4 months on the under sides of the plates when overgrown by *Ciona*, and for 5–7 months on the upper sides.

The period of *Ciona* dominance is another feature of South African waters, and may last for a varying time depending on local conditions. These organisms occur only on the under sides of objects and on vertical surfaces. The hulls of ships lying in dock for any period of time are soon covered with a heavy coat anything up to 12 in. in thickness (Plate XXXIII, fig. 1). The importance of these ascidians as fouling organisms, however, is lessened by the fact that they are easily detached and soon discarded by any vessel moving at speed.

Since both *B. algicola* and *Ciona* settle throughout the year, these two dominant communities can be expected to appear at whatever time an object is immersed, although likely to be more successful after the periods of maximum settlement in spring and autumn.

Unlike conditions in Great Britain (Wilson, 1925), there was no stage at which hydroids could be said to be dominant. They became plentiful only towards the end of Series II, when they were growing on the bodies of the *Ascidia*. That hydroids *can* form a dominant community is indicated by the fact that sheets of hydroids, particularly *Tubularia crocea*, have several times been observed on the hulls of ships, at periods varying from 5 months to 4 years after dry-docking. On the raft described below there

was a rich growth of *Tubularia* 6–7 weeks after launching. In this case it occurred concurrently with *Balanus algicola* and before the period of *Ciona* dominance. In general, the presence of a hydroid phase of dominance probably depends entirely on the seasons of settlement of the species and the available settling area.

The question now arises as to how far each community had approached a climax at the termination of these experiments. A good indication of a climax community can be obtained by the study of the population on the hulls of ships which have been in the water for long periods of time and which have not left the Cape Town area. For this purpose three typical vessels are selected, all of which had been in the water for longer than two years, and which are described as follows:

Example 1.

Name of vessel: "Labrus" (block-layer, S.A. Railways and Harbours).

History: 4 years 9 months in water. Stationary most of the time, with occasional movements within dock area. Examined 5/7/46.

Nature of fouling: A mixed population, mostly barnacles, tube-worms and mussels, forming a layer over 1 ft. over surface.

Abundant organisms: Hydroids: *Tubularia crocea* and *Kirchenpaueria pinnata.* Tube-worms: *Dasychone violacea* (Schmarda) and *Sabellastarte longa* (Kinb.). Barnacles: *Balanus maxillaris* and *B. algicola.* Mussels: *Mytilus crenatus* and *M. meridionalis.*

Other organisms present: Algae: *Ulva* sp., *Polysiphonia* sp. and *Delesseria ruscifolia.* Sponges: 1 species (undetermined). Coelenterates: *Bunodactis reynaudi* (M. Edw.), *Anthothoe stimpsoni*, *Bunodosoma capensis* (Lesson) and *Corynactis annulata* Verrill. Annelids: *Audouinia filigera* (D. Ch.), *Spirorbis borealis* and *Pseudonereis variegata* (Grube). Polyzoa: *Bugula calathus* and *B. avicularia* (Linn.). Barnacles: *Balanus trigonus.* Echinoderms: *Parechinus angulosus* (Leske). Ascidians: *Pyura stolonifera* (Heller), *Ciona* sp. and several compound species.

Example 2.

Name of vessel: "Steenberg" (steam whaler).

History: Laid up for 4 years in Saldanha Bay, then moved to Cape Town in May 1947. Examined 28/5/47.

Nature of fouling: Mixed population, mostly barnacles, mussels and sea-squirts, up to 1 ft. thick over whole surface.

Abundant organisms: Sponges: 1 species (undetermined). Anemones: *Anthothoe stimpsoni.* Polyzoa: *Bugula neritina* (Linn.). Barnacles: *Balanus maxillaris*, *B. trigonus* and *B. algicola.* Mussels: *Mytilus crenatus* and *M. perna* (Linn.). Ascidians: *Pyura stolonifera* and compound types.

Other organisms present: Algae: *Laminaria pallida* J. Ag. Sponges: 2 species (undetermined). Hydroids: *Obelia dichotoma.* Polyzoa: *Membranipora* sp., *Bugula calathus* and *B. avicularia.* Molluscs: *Anomia* sp. Echinoderms: *Parechinus angulosus.* Ascidians: *Ciona* sp.

Example 3.

Name of vessel: Union Defence Force barge.

History: Over 2 years in water. Passed backwards and forwards between Robben Island and Cape Town, with long periods in dock. Examined 6/2/48.

Nature of fouling: Mixed population, mostly sponges, barnacles, ascidians and weed. Patchy in distribution, but mostly 1–2 in. thick, with longer weeds reaching a length of $2\frac{1}{4}$ ft.

Abundant organisms: Algae: *Ulva* sp., *Pterosiphonia cloiophylla* (Ag.). Sponges: 1 species (undetermined). Hydroids: *Tubularia* sp. (probably *T. crocea*) and *Kirchenpaueria pinnata.* Polyzoa: *Bugula calathus.* Tube-worms: *Dasychone violacea.* Isopods: *Limnoria lignorum* (Rathke). Barnacles: *Balanus maxillaris.* Ascidians: *Ciona* sp.

Other organisms present: Algae: *Laminaria pallida* and several red species. Sponges: 2 species (undetermined). Hydroids: *Campanularia calceolifera* Hincks. Polyzoa: *Lepralia ? pallianassa* and *Watersipora cucullata* (Busk). Tube-worms: *Spirorbis borealis, Hydroides* sp. and various other free-living forms. Barnacles: *Balanus algicola* and *B. trigonus.* Mussels: *Mytilus meridionalis.* Ascidians: *Ascidia* sp., *Pyura stolonifera* and several compound species.

For the consideration of a climax community it is necessary to disregard *Balanus algicola* and *Ciona*, since both are shortlived forms, and when present at this stage in the growth are due to recent settlements growing on the surface of other organisms. Hydroids, too, though typically present in large numbers, are usually attached to other animals. A climax community in South African waters is typically of a mixed nature, with some or all of the following *basic* organisms (*i.e.* attached directly to the surface) present in recognisable numbers:

(*a*) The more permanent and slow-growing algae, such as *Laminaria.*

(*b*) Sponges.

(*c*) Anemones, generally *Anthothoe stimpsoni* and *Bunodactis reynaudi.*

(*d*) Tube-worms: *Dasychone violacea* and *Sabellestarte longa. Hydroides* is comparatively rare in South African waters, *Spirorbis* can be disregarded for the same reasons mentioned above.

(*e*) Polyzoa: various branching types.

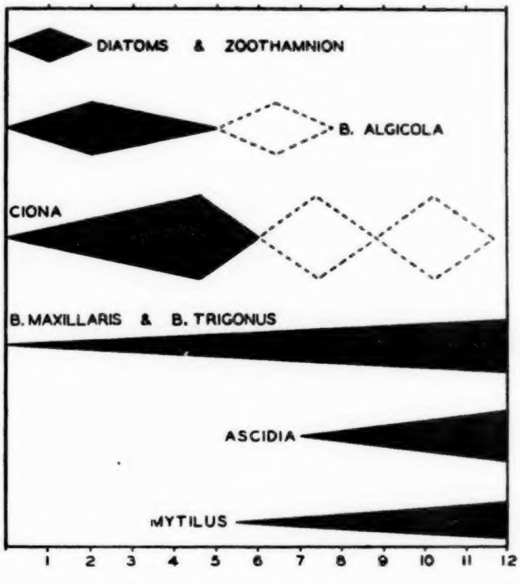
(*f*) The slower-growing and larger barnacles, namely *Balanus maxillaris* and *B. trigonus.*

(*g*) Mussels: *Mytilus crenatus, M. perna* or *M. meridionalis.*

(*h*) Ascidians of the hardy and resistant type, such as *Pyura stolonifera, Ascidia* and various compound forms.

To return to the experiments described in this connexion, it may be noted that in Series II several of these "basic" organisms were present towards the end of 10 months' immersion, namely *Ascidia, Balanus maxillaris* and *B. trigonus, Bugula calathus* and *Mytilus crenatus.* It may be thus concluded that at this time the community was approaching its climax.

In Series III, however, after 11 months' immersion, although a few of these "basic" organisms were present, namely *Balanus maxillaris*, *B. trigonus*, *Mytilus meridionalis* and *M. crenatus*, the population did not have the appearance of a climax community, as it did not form a complete covering to the plates and was sparse and scattered. Possibly if continued



TEXT-FIG. 6.—Diagram illustrating the typical succession which might be expected to occur in Cape Town waters over a period of 12 months. The scheme is of course dependent on the breeding seasons and subject to considerable variation. Possible repetitions of the *Balanus algicola* and *Ciona* periods of dominance are indicated by dotted lines.

longer another *Balanus-Ciona* community would have intervened before the climax.

In text-fig. 6 a plan has been constructed to give a general idea of the course of succession over a typical period of 12 months. Variations will of course occur, depending on the seasons of settlement and local conditions. Hydroids have not been included since they are so extremely variable.

It remains to mention briefly the importance of algae in the fouling succession. The plates which have been used so far have all been immersed at a depth of over 6 ft. below Low Water Springs; too deep apparently

for the quicker-growing algae, for the extreme paucity of algae was one of the remarkable features of the experiments. On the hulls of ships algae are abundant only near the water-line to a depth of about 3 ft. Had these plates been immersed closer to the water-level the quicker-growing algae would undoubtedly have played an important part in the fouling succession, and might have interfered with the periods of *Balanus algicola* and *Ciona* dominance. (See also p. 435.)

In conclusion a few words are necessary concerning the term "succession". In this paper the term has been used loosely to indicate the normal sequence of communities, but does not necessarily mean a causal succession, in which one community is definitely dependent upon a predecessor for its establishment and success. The successive dominance of the *Balanus algicola* and *Ciona* communities is not considered to be an example of causal succession, since both organisms can settle on freshly immersed surfaces, but is due simply to the fact that the two communities reach maturity within different periods of time. The same applies to the final attainment of a climax community. The sequence of many communities, *e.g.* hydroids, is largely dependent on the breeding seasons. Only two definite examples of causal succession have been observed. One is that of *Mytilus*, which form is unable to establish itself successfully on smooth uncolonised surfaces. In Series II, described in the first part of this section, the large settlements of mussels on the plates during the months February–April were unsuccessful colonisers and soon disappeared. At the same time, however, other mussels settled on the frame to which the plates were attached and grew successfully, reaching a length of 5–6 cm. by the end of June, when they formed dense clusters attached to any angle or irregularity in the frame. It appears that a more adequate protection was offered here than amongst the empty and crumbling barnacle shells and the loosely hanging *Ciona*.

Another example of causal succession was provided by the community of polychaet worms, which was so noticeable a feature of Series III described above. Such a community never appears on a smooth plate, but only after the surface has been made irregular by the attachment of barnacles. Similar types of community have been recorded by Fuller (1946) in Maine, U.S.A. (dominant species *Polydora ciliata*), and by Graham and Gay (1945) in California (dominant species *Polydora ligni*). Neither author makes mention of the necessity of a previous community, although Fuller states that the worms "eliminated other communities with the exception of the common mussel".

Both these communities are thus largely dependent on the nature of the substratum, and if the suitable substratum is provided by a previous group of animals, then true causal succession may be said to occur.

Rates of Growth.

It is not possible to give any consecutive account of growth-rates, since at no time were any same individuals watched and measured throughout the whole course of their development. The following records, however, may give a rough indication of the time taken by the more important species to grow and reach maturity.

Tubularia crocea can produce heads bearing gonophores with a total height of 2·2 cm. in 35 days. Heads of only 1·05 cm. in height may also bear gonophores. One colony grew rapidly during the spring months, reaching a height of 5·5 cm. in 49 days, reproduced actively, and then died down during mid-summer, leaving only the stalks.

Kirchenpaueria pinnata can produce upright colonies of 1·4 cm. in height in a period of 33 days, and colonies 2·6 cm. in height in 94 days, which latter is approximately its full size.

Obelia geniculata can produce fruiting colonies of 1 cm. in height in a period of 29 days.

Obelia dichotoma can produce fruiting colonies of 1·6 cm. in height in a period of 35 days, and can reach a height of 4·5 cm. in 198 days.

Bugula calathus can reach a height of 1·2 cm. in 35 days. Its maximum height appears to be about 3·5 cm., as seen on ships' hulls.

Balanus algicola grows at a faster rate during the spring months of September and October, when it may reach a diameter of 7–8 mm. and a height of 4–6 mm. in about 35 days, which is its normal adult size. At other times of the year it normally reaches a diameter of only 4–5 mm. and a height of 2–3 mm. in the same period of time.

Balanus maxillaris is the largest barnacle in South Africa, and has been found to reach a maximum diameter of 5·5 cm. and height of 7·0 cm. on ships' hulls. It has never grown as large as this on the experimental plates and possibly takes more than a year to mature.

The following figures will give an idea of the growth rate:

Period of Growth.	Max. Diameter.	Max. Height.
36 days	0·8 cm.	0·5 cm.
63 ,,	1·15 ,,	0·95 ,,
94 ,,	1·5 ,,	1·2 ,,
128 ,,	1·7 ,,	1·8 ,,
163 ,,	1·9 ,,	2·1 ,,
436 ,,	4·0 ,,	5·2 ,,

Balanus trigonus is a smaller and flatter barnacle. The largest specimens seen on ships' hulls had a diameter of 2·1 cm. and height of 1·3 cm. The rate of growth on experimental plates is as follows:

Period of Growth.	Max. Diameter.	Max. Height.
34 days	0·65 cm.	0·3 cm.
70 ,,	1·1 ,,	0·9 ,,
128 ,,	1·3 ,,	0·65 ,,
140 ,,	1·45 ,,	0·75 ,,

Mytilus meridionalis is the only species of mussel which grew successfully on the plates. The rate of growth is as follows:

Period of Growth.	Max. Length.
35 days	0·5 cm.
105 ,,	1·3 ,,
140 ,,	2·3 ,,
175 ,,	4·6 ,,
274 ,,	7·8 ,,

When mature this mussel may reach a length of over 8 cm.

The ascidian, *Ciona*, is able to grow and reach maturity in a very short period of time, as shown by the following figures. Measurements were taken when the animals were lax and expanded.

Period of Growth.	Max. Length.
35 days	2·8 cm.
63 ,,	7·6 ,,
94 ,,	15·5 ,,
128 ,,	15·8 ,,

When hanging from the under sides of ships, *Ciona* may reach a length of 30 cm.

Zonation.

To determine the vertical zonation of the fouling organisms, plates were suspended from the side of a raft as described on p. 417. In all, three series of experiments were performed, which will be designated IV, V and VI. The raft was so constructed that some of the plates could be suspended through the centre and covered with a hatch, thus reducing the light considerably (Plate XXXIII, fig. 2).

In Series IV, 10 plates were suspended at regular intervals at depths varying from 7½ in. above the water-line to 49½ in. below. These were examined on 26/1/49 after an interval of 13½ weeks. For the same period a strip of steel (representing Series V) measuring 7 in. by 5 ft. was suspended vertically with the top just above the water-level. This strip was covered by the hatch and acted as a control to Series IV.

In Series VI a wider range was covered, and 10 plates were immersed at regular intervals from water-level to a depth of 9 ft. below. These were examined on 23/2/49 after 9½ weeks.

The results of these experiments were not particularly striking, and there was surprisingly little obvious zonation to be seen. They will therefore not be quoted in detail, but it will merely be attempted to summarise the main points of interest and to bring these into line with other observations on the hulls of ships.

The most striking feature was a rich growth of algae which covered the plates in Series IV and VI to the exclusion of practically all else, though not present on Series V covered by the hatch. These included chiefly *Enteromorpha* and *Ceramium*, but also *Ulva*, *Polysiphonia* and *Nitophyllum*. Of these, the green algae tended to be more abundant close to the water-line, and the reds more or less evenly distributed down to a depth of 7½ ft., below which they become scarcer. It was surprising that no algae occurred on the plates in Series I, II and III (with the exception of *Nitophyllum*, and that only in very minute quantities), where the depth ranged from approximately 6¼ to 10½ ft. below Low Water Springs. The only reason for this could be a difference in the illumination, since the frame was hanging hard against the wall, and the raft moored well away from the side.

A very much more definite impression was gained from the hulls of ships in dry dock, where the green algae (*Ulva* and *Enteromorpha*) were limited to a narrow band extending down to about 3 ft. below water-level. Reds and browns, including *Polysiphonia*, *Pterosiphonia cloiophylla*, ? *Nitophyllum venosum*, *Ceramium*, *Scytosiphon lomentarius*, *Ectocarpus*, *Gigartina radula* and *Laminaria pallida*, occurred irregularly on the sides of vessels, whereas the under surfaces bore animal growths only.

The fauna showed little obvious zonation in these experiments. There was, however, a tendency for the barnacle *Balanus algicola* to be more numerous close to the water-line, and *B. trigonus* at deeper levels from 5½ ft. down. *Ciona* showed a definite preference for the less well-illuminated regions and occurred abundantly on the covered strip in Series V, where it was most dense in an area from 6 in. to 2 ft. below water-level (Plate XXXII, fig. 4).

To summarise, algae occur only in well-illuminated areas, the green algae close to the water-line, reds and browns to a varying depth below depending on local conditions. Both may occur on the sides of ships. Barnacles, hydroids and mussels are independent of the light factor and may occur in well-lit or shaded areas at almost any depth, although individual species probably have an optimum level. All three occur on the sides and bottoms of ships, hydroids being more common on the bottoms, and mussels on irregular surfaces such as gratings, grids, etc. All three

have been seen to occur in completely darkened regions such as condensers of ships, pipes, etc. Finally, *Ciona* definitely avoids light, occurring only on the under sides of plates, the bottoms of ships, and on vertical surfaces in darkened areas.

Wood-boring Organisms.

Though few ocean-going wooden vessels are in use these days, wood-boring organisms are still of vital importance from the point of view of piles, barges, yachts, etc., and thus deserve mention in a work of this type. In Cape Town Docks four wood-boring organisms have so far been encountered, namely the Teredinidae *Bankia* sp. and *Lyrodus* sp., the "gribble" *Limnoria lignorum* (Rathke), and the boring amphipod *Chelura terebrans* Phil.

Bankia occurs abundantly in any wooden structure submerged in the water. Well-grown specimens of over 15 cm. in length have been collected from special frames immersed for this purpose after a period of 15 weeks. *Limnoria* is common in most wooden structures, and has been found in the wooden barge described on p. 430, and in the raft used during the experiments. *Chelura* has been observed only in the wood of the raft.

The Effect of Anti-fouling Paint.

To test the effect of a typical anti-fouling paint in South African waters, control plates were included in some of the experiments. The paint, applied over the usual two coats of anti-corrosive, was one commonly used on naval vessels in Cape Town. Analysis showed that it contained 1·5 per cent. As_2O_3, 13·5 per cent. Cu, 15·2 per cent. Cu_2O, and a trace of metallic mercury.

Pyefinch (1946) described a method for assessing the value and life of an anti-fouling composition, but since in South Africa there are not only different climatic conditions but completely different species involved, comparisons are extremely difficult. Consequently in Table II the numbers of organisms over a typical yearly period dating from 4/3/47 to 31/3/48 are quoted in detail. In the case of *Mytilus* and *Anomia*, where accurate counts were not taken, Pyefinch's rating has been applied.

It would appear in the first place that the fouling, even on non-toxic surfaces, is infinitely heavier than that occurring in British waters, as might reasonably be expected in a warmer latitude. However, it has been noted by both Visscher (1927) and Weiss (1948) that heavy fouling is typical of built-up harbours where bulkheads, pilings, etc., provide suitable attachments for adult forms which in turn produce a high concentration of larvae.

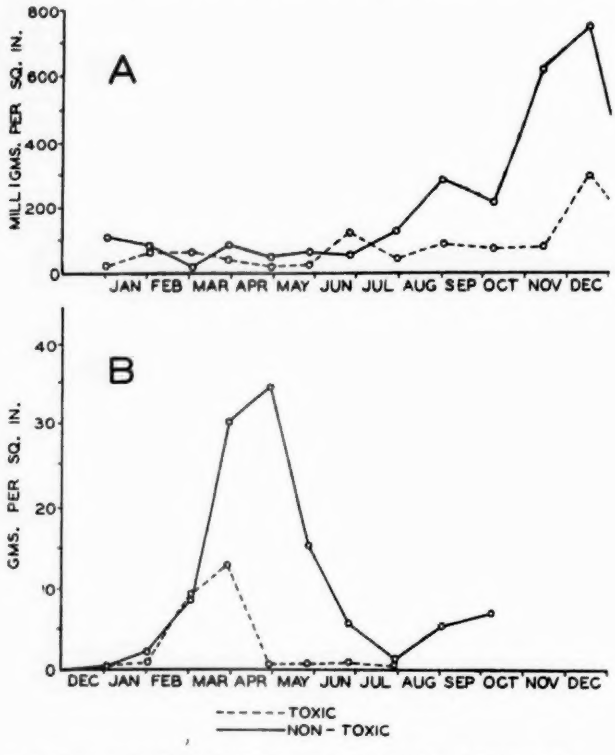
In the second place, the fouling occurring on the toxic surfaces is

TABLE II.—NUMBERS OF ORGANISMS PRESENT ON PLATES EXPOSED FOR PERIODS OF APPROXIMATELY ONE MONTH EACH.

Period of Exposure.	Hydroids.		Spirorbis.		Bugula.		Balanus.		Mytilus.		Anomia.		Ciona.	
	A.C. only.	A.C. + A.F.	A.C. only.	A.C. + A.F.	A.C. only.	A.C. + A.F.	A.C. only.	A.C. + A.F.	A.C. only.	A.C. + A.F.	A.C. only.	A.C. + A.F.	A.C. only.	A.C. + A.F.
3/12/46– 3/ 1/47 .	1	3	A	A	–	–	2436	1350	–	–	–	–	55	–
3/ 1/47– 3/ 2/47 .	–	–	A	A	–	–	1668	3801	–	O	–	–	O	189
3/ 2/47– 4/ 3/47 .	–	–	VF	1176	–	–	597	126	VA	A	O	O	–	–
4/ 3/47– 1/ 4/47 .	–	–	1386	6427	–	1	2058	92	R	R	R	R	21	63
1/ 4/47–29/ 4/47 .	–	–	1008	–	–	–	66	–	–	–	–	–	968	–
29/ 4/47–27/ 5/47 .	5	–	609	110	–	–	3339	–	–	–	–	–	4452	–
27/ 5/47–26/ 6/47 .	5	–	567	616	–	–	2940	1342	–	–	–	–	3549	777
26/ 6/47–30/ 7/47 .	–	–	39	1072	–	–	–	802	–	–	–	–	–	1
30/ 7/47– 4/ 9/47 .	27	–	504	798	–	–	3339	366	–	–	–	–	74	45
4/ 9/47– 9/10/47 .	49	5	945	1638	4	3	6825	4515	–	–	–	–	27	17
9/10/47–14/11/47 .	104	–	294	–	2	1	10164	3945	VF	–	–	–	90	–
14/11/47–19/12/47 .	4	64	101	–	2	–	5292	4830	A	A	O	–	1281	989
19/12/47–23/ 1/48 .	–	–	44	–	4	–	2793	1701	O	F	F	–	89	–
23/ 1/48–26/ 2/48 .	4	–	54	–	2	–	5859	609	VR	F	F	F	11	–
26/ 2/48–31/ 3/48 .	2	–	12	–	2	6	8694	5019	O	O	–	–	62	1680
31/ 3/48– 4/ 5/48 .	315	X	17	X	8	X	7161	X	R	X	–	X	491	X
4/ 5/48– 2/ 6/48 .	5	X	13	X	6	X	9141	X	O	X	VR	X	861	X
2/ 6/48–24/ 6/48 .	–	–	13	8	–	–	77	261	–	–	–	–	O	O
24/ 6/48–28/ 7/48 .	–	–	23	–	–	1	656	19	–	–	–	–	1	–
28/ 7/48–30/ 8/48 .	6	–	49	–	1	–	186	4	–	–	R	–	59	–
30/ 8/48–29/ 9/48 .	–	–	44	–	2	–	715	974	–	–	–	–	861	–
29/ 9/48– 1/11/48 .	9	4	48	14	8	–	1102	2751	R	VR	R	VR	93	651
1/11/48– 2/12/48 .	1	–	7	–	2	–	574	58	–	VR	R	–	11	–
2/12/48– 5/ 1/49 .	–	–	46	–	–	–	226	151	–	–	VR	–	47	–

A.C., anti-corrosive paint; A.F., anti-fouling paint. Surface area of plates = 42 sq. in. (or approx. 271 sq. cm.).
Symbols : –, absent; VR, very rare; R, rare; O, occasional; F, frequent; VF, very frequent; A, abundant; VA, very abundant; X, no records taken.

sufficient to class this particular paint as definitely inadequate according to Pyefinch's standards, although it is possible that the same paint used in British waters might be perfectly adequate. Of all the organisms concerned, with the single exception of *Obelia*, there was none virtually



TEXT-FIG. 7.—Diagram illustrating the effect of anti-fouling paint.

A. The seasonal fouling during the year 1947. The graph for the non-toxic surface is taken from the same records used in text-fig. 1 A.

B. The accumulative fouling over a period of 10½ months, starting 3/12/46. The graph for the non-toxic surface is taken from the same records used in text-fig. 5 A.

unable to settle on the toxic surface within the period of one month, and against which the paint could be said to offer complete protection.

It is also clear, however, that the anti-fouling paint did provide *some* protection, but that this protection was quantitative rather than specific. This quantitative effect is shown graphically in text-fig. 7 A, which illustrates the seasonal fouling in weight for the year 1947, and also in Plate XXXII, fig. 1.

Further information is provided by text-fig. 7 B, which shows the accumulation of fouling on plates immersed for increasing periods of time. This figure shows an interval of about 1 month on the non-toxic surface before substantial increase in weight occurs, this period being prolonged to about 2 months on the toxic surface. After this there is a period of about 2 months on the non-toxic surface and 1 month on the toxic surface with relatively slow increase in weight, during the latter part of which the two graphs run parallel. If this diagram be compared with text-fig. 6 it will be seen that this was the time during which the barnacle *B. algicola* was the dominant organism, so it may be safely concluded that this species is outstandingly resistant to the poisons contained in the anti-fouling paint. This conclusion is substantiated by the figures in Table II. Here the counts include 3 species of barnacles, *Balanus algicola*, *B. maxillaris* and *B. trigonus*, but of the three *B. algicola* was by far the most abundant.

Following this period of comparatively slow increase in weight there is a period of very rapid increase on the non-toxic surface which is not repeated on the toxic surface. This is the period of *Ciona* dominance, and it thus appears that the settlement and growth of this organism is impeded to a greater extent by the toxins of the anti-fouling paint, but, as has been mentioned on p. 428, *Ciona* is only significant as a fouling organism when vessels are in dock for long periods of time.

Fouling Communities on Ships.

During the course of three years a total of 26 vessels was examined in Cape Town harbour and one in Simonstown dockyard. Of these, 13 had restricted their movements to the Union of South Africa, and of the remainder, although all had visited foreign ports at some time of their voyage, most bore a preponderance of animals typical of the Cape Town area. A full list of species cannot be included here since the identifications are not complete, but will be published at a later date.

The type of fouling on these vessels varied considerably. In some cases the population was obviously dominated by one or two groups of animals which established a definite type of community; in others the population was so mixed that no particular type of organism could be said to be dominant. It has been possible, thus, to select a number of communities which can be taken as representative of South African waters. These are listed below, together with suggestions as to their place in an ecological succession.

1. *Barnacle Community.*—Observed on 5 vessels, which had been in the water for comparatively short periods of time varying from 3½ to 9 months. Such a community usually consists mostly of sessile barnacles, including

the species *Balanus algicola*, *B. maxillaris*, *B. trigonus* and *B. amphitrite* Darwin. Occasionally stalked barnacles may be in the majority, e.g. *Conchoderma auritum* Linn., *C. virgatum* Spengler, *Lepas* spp., but the two types may be mixed in more or less equal quantities. With the barnacles may occur smaller numbers of other organisms, particularly hydroids, polyzoa, ascidians and weeds. This type of community is considered on the evidence of experimental work to be of a transitory nature and likely to give place to one of the following types.

2. *Barnacle + Ciona Community.*—Observed on 3 vessels, in the water for 7, 8 and 11½ months respectively. In this community the most common barnacle is *Balanus algicola*, although other species may also occur. The *Ciona* are usually young and immature, and the community appears to be midway between the barnacle and the *Ciona* type. Once again a smaller number of other organisms may occur.

3. *Ciona Community.*—Observed on 4 vessels, in the water for periods varying from 5 to 14 months. The *Ciona* are always large and mature and occupy practically all the available space. A few barnacles usually manage to subsist amongst them, and occasionally a few *Mytilus* and polyzoa. The *Ciona* community is only to be found on the *bottoms* of vessels (Plate XXXIII, fig. 1); in the case of flat-bottomed crafts a *Ciona* community may be present on the bottom and some other type (e.g. *Mytilus*, or mixed) on the sides. It is considered that this community may develop on recently immersed vessels, or may replace an earlier barnacle community.

4. *Barnacle + Hydroid Community.*—Observed on 2 vessels, in the water for 8 and 15 months respectively. This is a very typical community, consisting of numerous sessile barnacles of the 4 species mentioned above, with a feathery carpet of hydroids growing over and amongst them to a height of about 2 in. Larger animals are conspicuously absent, though a few polyzoans, small mussels, ascidians and weeds may occur. In both cases the dominant hydroid was *Tubularia crocea*, though other species, such as *Gonothyraea loveni* and *Campanularia* sp., were also abundant. It is obvious that such a population has succeeded a barnacle community, since the hydroids have attached themselves on top of the barnacles. The fact that a pure hydroid community has never been observed is possibly due to the poorer resistance of these forms to the anti-fouling paints commonly used.

5. *Mytilus Community.*—Observed on 2 vessels, both in the water for approximately 1 year. Three species of mussels occur, namely *Mytilus meridionalis*, *M. crenatus* and *M. perna*, of which the first named is easily the most common. Such a community consists of dense layers of mussels seated on one another to a depth of about 9 inches. Various

other organisms, such as barnacles, polyzoans and *Ciona*, may attach themselves to the mussels. The position of this community in the ecological succession is not clear, but in one case at least the *Mytilus* community was seen to follow after a *Ciona* one. Whether it is a permanent or a transient population has not been determined.

6. *Ostrea Community.*—This is apparently a rare type of community in the Cape Town area, and has been observed on only one vessel, which had been in the water for one month and had not left the docks during this period. It is noteworthy that the vessel had been scraped, but not painted, at her last dry-docking, which would possibly account for the rapid fouling. The oysters responsible were of the species *Ostrea gasar* (Adanson), and had reached a maximum length of 2·9 cm. Amongst them were barnacles (*Balanus amphitrite*), polyzoa and hydroids. A few *Hydroides norvegica* were also present.

7. *Tube-worm Community.*—Observed on 3 vessels, 2 in Cape Town docks and 1 in Simonstown dockyard, in the water for periods varying from 6½ to 11 months. All 3 vessels had recently come from the East, which suggests that the worms had been collected there, particularly as they have never been observed in any quantity in Cape Town. The worms responsible were *Hydroides norvegica* (Gunn.). Usually they form a thick coating 1–2 inches deep, with little room for other organisms, though in places barnacles, polyzoa and ascidians may find attachment between them, and hydroids (*Tubularia* and *Kirchenpaueria*) may grow over the surface.

8. *Mixed Community.*—This type of community invariably occurs on vessels which have been in the water for long periods of time. It has been observed on 3 vessels which had not been dry-docked for 4 years, and on several vessels in the water for periods varying from 1 to 2 years. It is considered to represent the climax community for this area, and 3 typical examples have already been described on p. 429. The population consists of slow-growing and long-lived forms, including various species of weeds, sponges, anemones, barnacles, mussels and ascidians, amongst which may shelter innumerable unattached forms such as polychaets, crabs, sea-urchins, etc. The population, in fact, is such as might occur on any submerged surface below low-tide level.

Comparisons with other Localities.

In Great Britain most of the recent work on fouling is to be attributed to the members of the Marine Station at Millport (Pyefinch, Bishop *et al.*), though work is also progressing at the Marine Paints Research Station, Brixham, under the direction of D. J. Crisp.

As has been mentioned on p. 436, the impression has been gained that

fouling is in general heavier in South Africa than in Great Britain. Comparisons, however, are difficult without direct observations, particularly as few published papers give sufficient data on density of population, temperatures, etc.

American workers have developed no system of rating comparable to that of Pyefinch (1946) in Great Britain, but accounts are given by Richards and Clapp (1944) and Pomerat and Weiss (1946) from Florida, Fuller (1946) from Maine, Graham and Gay (1945) and Scheer (1945) from California, and Walton Smith (1946) from Woods Hole. From these it appears that the fouling intensity varies considerably in different parts of the United States, with a tendency for heavier fouling in more tropical latitudes.

Fouling in Hawaii has been described by Edmondson and Ingram (1939) and Edmondson (1944), and fouling in Australia by Allen and Wood (1950). In both localities it appears to be comparatively heavy and on a par with that in Cape Town, although in Hawaii the nature of the fouling is rather different, consisting largely of the tube-worm *Hydroides*.

Most authorities consider that the fouling intensity is closely linked with temperature variation, and this agrees with the published records. In regions where the fouling intensity appears to be less than in Cape Town the monthly mean temperatures reach a minimum of 9° C. or less. Thus, Bishop (1946) gives a range of 0–17·0° C. in various parts of Great Britain, Fuller (1946) records a range of 4·4–16·1° C. in Maine (records only from May to October), and Graham and Gay (1945) give a yearly range of 9–22° C. in California.

Fuller (1946) and Graham and Gay (1945) suggest that the optimum temperature for fouling settlement is 15° C. or over, but this of course applies only to their local species. In most areas where fouling is heavy the maximum monthly temperature is considerably higher than this—*e.g.* Richards and Clapp (1944) report a range of 58–81° F. (or 14·5–27·3° C.) from Florida, Edmondson and Ingram (1939) a minimum of 20° C. and a "normal" of about 25° C. from Hawaii, and Allen and Wood (1950) an annual temperature range of about 14·2–23·1° C. from Cronulla, Australia.

It is noteworthy that although the fouling in Cape Town appears to be comparable with the three latter regions, the maximum mean monthly temperature is considerably lower, the range being from 11·1 to 15·0° C. It is suggested, therefore, that an important factor favouring fouling in Cape Town is the small range of temperature throughout the year.

Summary.

Investigations on the fouling organisms in Table Bay Harbour were conducted over a period of three years, partly by examination of ships in

dry dock, and partly by immersing experimental plates at regular intervals for known periods of time.

The most important fouling organisms in Cape Town include hydroids, polyzoa, tube-worms, mussels, barnacles and ascidians. The seasons of settlement of the most common species were determined, and it was found that in general the fouling is heaviest in spring and in autumn, although seasonal variation in fouling is never so marked as in Great Britain. The nature of the fouling varies considerably from year to year, depending on local conditions.

There is no clear correlation between water temperatures and fouling, although at times a rise in the fouling settlement appears to follow a rise in temperature. Owing to local currents and winds, the average monthly water temperatures in Cape Town Docks are higher in winter than in summer, and the total range is small, varying between 11·1 and 15·0° C. during the period 1946 to 1949. This small range is considered to be a factor favouring fouling settlement, which is heavy in this area.

In the succession of organisms in a fouling community, an early phase of dominance by *Balanus algicola* followed by one by *Ciona* is invariably present. Both organisms may settle at any time of the year and both are shortlived. The period of *Ciona* dominance may be repeated several times, or may be followed by a mixed population of more stable organisms which finally establish themselves as a climax community. A period of hydroid dominance may intervene at some stage, but is not typically present, and when it occurs is largely dependent on the breeding seasons of the species.

True causal succession is rare, but may occur in the case of *Mytilus* and polychaet (Spionid) communities, both of which require an irregular substratum for successful establishment.

Rates of growth of some of the more common species are given.

Vertical zonation was not marked on the experimental plates, but was more obvious on the hulls of ships. Green algae are usually abundant near the water-line, reds and browns are found at a deeper level on the sides of ships, and only animal forms occur on the under sides. Whereas algae occur only in the presence of light, some animals, *e.g.* barnacles, mussels and hydroids, are indiscriminate, and others again, e.g. *Ciona*, tend to avoid light.

Experiments with single anti-fouling paint show that, as far as a comparison is possible, fouling in Cape Town waters is heavier than in Great Britain, and the toxins in the paint provide a less adequate protection. Particularly resistant to the toxins is the common barnacle *Balanus algicola*.

The fouling communities which occur on ships' hulls are classified into 8 main categories, and suggestions are made as to their place in an ecological succession.

ACKNOWLEDGMENT.

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EXPLANATION OF PLATES.

PLATE XXXII.

Fig. 1.—Two plates after an exposure of 5 weeks, examined 14/11/47, and illustrating the early stages of a Balanoid community. A, with anti-corrosive paint only; B, anti-corrosive plus anti-fouling. Photo: G. J. Broekhuysen.

Fig. 2.—Two plates after an exposure of 9 weeks, examined 3/2/47, and illustrating a well-advanced community of *Balanus algicola*. A, with anti-corrosive paint only; B, anti-corrosive plus anti-fouling. Scale in inches. Photo: G. J. Broekhuysen.

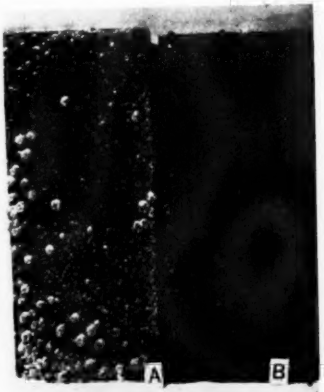
Fig. 3.—The apparatus used for holding the plates in experiments, Series I–III. The plates, each 3 × 7 inches, are shown in position. Photo: G. J. Broekhuysen.

Fig. 4.—The strip used in experiment Series V after an exposure of 13½ weeks. The strip is covered by a young *Ciona* community, most pronounced from 6 to 24 in. below water-level. In the barer regions scattered barnacles, polyzoa and *Tubularia* stalks are visible. Photo: G. J. Broekhuysen.

PLATE XXXIII.

Fig. 1.—A well-advanced *Ciona* community on the hull of a ship in dry dock. Photo: W. J. Copenhagen.

Fig. 2.—The raft used for the suspension of plates in experiments, Series IV–VI. Photo: E. Sandison.



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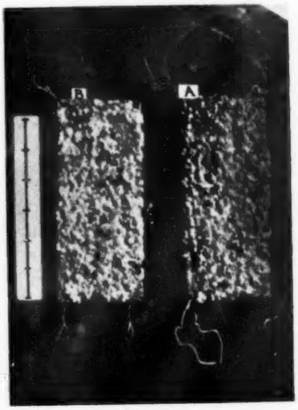

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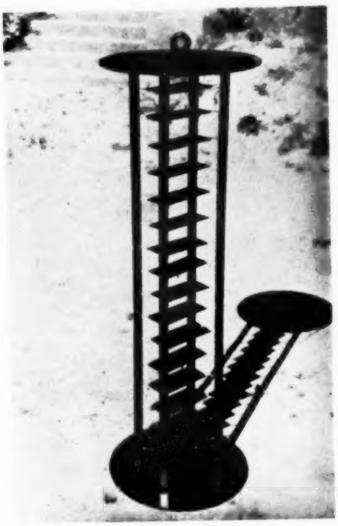

Fig. 3.

Fig. 4.

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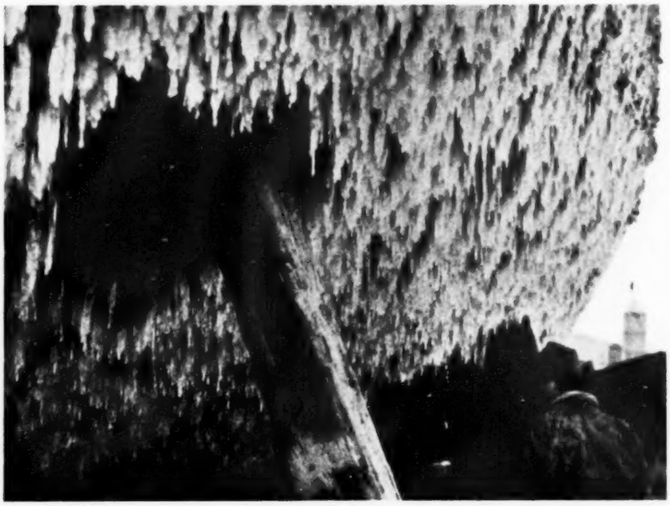

Fig. 1.

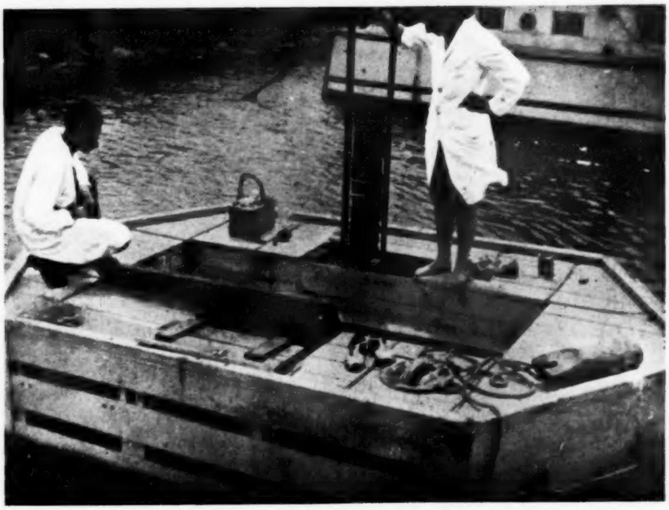

Fig. 2.

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THE LIFE-HISTORY OF *PHASIS ZEUXO ZEUXO* (L.)
(Lepidoptera: Lycaenidea).

By C. G. C. Dickson.

(With Plate XXXIV and two Text-figures.)

(Read March 21, 1951.)

ABSTRACT.

A comprehensive account is given of the life-history, apparently not previously known, of the South African Lycaenid butterfly, *Phasis zeuxo zeuxo* (L.), with systematic descriptions and clear black-and-white figures, including details drawn under magnification, of the various stages.

The honey-gland and the function of the retractile tubercles of the larva are discussed in the early portion of the paper. All the stages, including each larval instar, are recorded separately. Observations are given on the habits of the larva and the imago, with reference to the time of appearance and flight-period of the butterfly and the probability of its being single-brooded. Localities are noted, and the recently ascertained extensive range of the butterfly eastwards of Cape Town is mentioned.

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INTRODUCTION.

The life-history of this rather plentiful though localised Lycaenid butterfly, described as early as 1764,* appears to have been unknown until recently, when, with a view to recording the early stages, eggs of the species were procured on the lower mountain slopes above St. James, Cape Peninsula, on 1st December 1947.

Female butterflies frequenting bushes of the common composite, *Chrysanthemoides monilifera* (L.) T. Norl., were followed closely and were

* *Papilio Zeuxo* L., Mus. Lud. Ulr. Reg., p. 331, n. 149 (1764) and Syst. Nat., I. 2, p. 789, n. 231 (1767). Descriptions of the species are given also in Trimen's "Rhopalocera Africae Australis" (Pt. II, pp. 262–263, pl. 5, fig. 2) and "South African Butterflies" (Vol. II, pp. 171–172), Seitz's "Macrolepidoptera of the World" (Vol. XIII, p. 431) and Murray's "South African Butterflies: A Monograph of the Family Lycaenidae" (p. 107, fig. 52).

observed to lay eggs on the leaves of the plants, in one case an egg being laid also on the bark of a main stem. Both fresh and withered leaves were used for oviposition and as a rule eggs were laid singly, but on one occasion two were placed side by side on a leaf.

Subsequently, larvae in the first to fourth instars were discovered on plants of *Chrysanthemoides incana* (Burm. f.) T. Norl. growing close to the seashore at Hottentots Huisie. They were very effectively concealed, frequently in dead curled-up leaves, and their colouring, flattened form and numerous lateral setae rendered them very inconspicuous. One or two pupa-cases were also found, well concealed, near the ground.

These larvae, which possess a honey-gland which first appears in the second instar, and is posteriorly placed in the dorsum of the tenth segment, and a pair of retractile tubercles in the eleventh segment, one on each side, in a simple form in the first instar and developing in successive instars, are associated with ants. The only ants seen on the food-plants were Argentine ants, and it is assumed that these ants attend the larvae in this particular spot, although this was not observed, but Argentine ants are known to "milk" the larvae of at least two other South African Lycaenids, i.e. *Cupido boeticus* (L.) and *C. thespis* (L.), in localities in which they have replaced native ants.

The function of the tubercles very definitely appears to be to protect the honey-gland and control insects approaching it. In the first instar, as there is no honey-gland, the tubercles are very simple though they are sometimes protruded, especially when a larva is disturbed, which points to the theory of protection.

When the honey-gland is developed and functioning, it is seen that the tubercles dust the vicinity of the gland with their long spines or hairs in quick, sharp beats, frightening or diverting unwanted insects. Observations made in the past on larvae of *Phasis thysbe brooksi* (Riley) have shown that on occasion the tubercles may be protective even where ants are concerned as, when ants were milking a larva, full extension of the tubercles disturbed them and the gland was allowed some respite from their attentions.

Some of my observations have been made in conjunction with Mr. Gowan C. Clark, of Port Elizabeth, who has also made extensive observations on the honey-gland and we have come to the same conclusion as to the function of the tubercles.

Egg.

The egg (figs. 1 and 2) is about 0·7–0·75 mm. in diameter and 0·43–0·53 mm. in height and is "bun-shaped". The cellular, mainly hexagonal, pattern is coarse over the greater part of the surface. The colour is creamy-

white, but may gradually become greyish white or pale grey, the inner part of the cells at first having a more or less dark yellow or yellow-green tinge.

Eggs hatched 11–13 days after they were laid, the larva emerging through an opening which it bites out of the crown of the egg.

Larva.

First Instar.

The larva on emergence (fig. 3: larva two days after emergence) is about 1·5 mm. in length, the body being rather broad and much compressed (fig. 4).

Head (fig. 5) dark brown, lightening towards the bottom, with a shiny surface and bearing white setae of different lengths.

Body light stone-coloured with, at first, dull vinous colouring on some of the earlier and later segments. Neck- and anal-shields dark brown. There are two rows of very obscure patches up to segment IX. Segment X bears two large prominent patches, widening posteriorly, and on the following area of the body the colouring is very extensive. As it develops, the larva assumes a somewhat dull yellow tint and may be partially tinged with dull green, the pattern becomes better defined, and two other longitudinal series of markings may be perceptible on each side, with some marking also under the lateral ridge. On a few of the segments there are minute double medio-dorsal spots. Extensive marking in the region of the tubercles includes, in time, a central projection in front of and contiguous with transverse colouring a little anterior to the anal-shield, and two smaller projections.

The tubercles (fig. 3*a*) are white, each bordered on the inner side with three short, black setae with broad, circular, translucent-white ends, and on the outer side of each is a spine-type seta which curves back over the terminal segment. Each tubercle is provided with two pale-coloured setae, which become visible when the tubercle is extended.

The setae are short to rather long dorsally, a few anterior ones being very long, and on the ridge laterally and at the extremities they are fairly long to very long. The dorsal setae, which beyond seg. III nearly all curve over in a posterior direction, are mostly principally black with white ends, two very long anteriorly-directed ones on II being more white than black, as are the very long ones on the ridge, the shorter lateral ones nearly all being entirely pale-coloured. The general arrangement of the setae is shown in fig. 3, and the setae on one side of seg. VII are represented in fig. 6, their disposition being the same on other segments from IV to IX. In fig. 6 an extremely short black seta is obscured by the fourth visible seta from the top of the body and a small ring is obscured by the main

lateral seta. Two fairly short pale setae on the posterior edge of seg. X are believed to be erectile.

The young larva when feeding makes a minute hollow in a leaf and between the feeding periods sometimes rests with its head in the hollow, and after several days a little furrow has been produced and the larva rests in this with the long lateral setae spread out over the surrounding leaf-surface, the setae acting as a shadow-breaker which helps to camouflage the edges of the furrow. The duration of the first instar exceeded three weeks.

Second Instar.

The larva now begins to resemble the final instar larva.

Head mainly very dark brown, nearly black, and with the setae considerably more numerous and relatively shorter than in the first instar. Labrum orange-brown, the skin above it whitish grey.

Body of a general dull pale green colour, tinged or marked towards the ends with dull vinous and with faint indications of longitudinal lines darker than the ground-colour: a medio-dorsal pair, two very sinuous lines to each side of them and a less distinct indication of a line above the lateral ridge. On seg. X there is vinous colouring transversely, anterior to the honey-gland, which is now present, and prominently at each end. On the following area of the body it occurs mainly in the form of a short transverse streak in front of each tubercle-casing confluent with colouring round the casing, each streak having a very fine projection in front of it; a transverse streak between the casings with two short forward projections centrally; and between this and the anal-shield broad transverse colouring posteriorly attenuated outwardly and with fine projections to the colouring in front of it. Behind the anal-shield vinous colouring occurs in the form of an arc. Neck- and anal-shields very dark brown though partly pale-coloured, the former with a pale central division.

The honey-gland is well concealed when the opening is contracted. Transversely next to the opening are some small, very short, pale, translucent setae with broad, circular, flattened ends.

The tubercles now have short, dark brown chitinous casings, on the rim of each of which are some seven upright spines with projections spread out round their ends.

The setae now scattered numerously over the upper surface of the body are of a small specialised type with projections round their ends, the projections widening slightly outwardly (see fig. 10). These setae are translucent-white or black, but mainly white. On the anal-shield they are mostly black. The setae of ordinary type which are now confined to the sides and ends of the body (apart from fine setae which may occur on

the venter) are appreciably more numerous though relatively shorter, the length of the longest being approximately equal to the width of the body. The usual number of main upper lateral setae on each side of segs. II–X is four to five. In addition to the long setae many short ones occur laterally and at the ends of the body. The setae, which bear numerous small barbs, are either pale-coloured or (many larger ones) dark from the bases and then pale, some, especially at the anterior end where dark ones are most common, being almost wholly dark. In later instars their colour lightened, but some further darkening ultimately took place.

The duration of the second instar was not ascertained.

As only a gradual change takes place in successive instars between the second and final instars, full descriptions of the intervening instars are unnecessary. The setae increase in number with each moult.

Third Instar.

White specialised setae occur more prominently than before centrally in front of the neck-shield, with many on the shield also. Some change is noticeable in the markings towards the anal end. Neck- and anal-shields pale brown, with some very dark brown marks. On the neck-shield were noticed also some small prominences and very short, plain setae.

The tubercle-casings are yellowish brown with dark brown rims, the upright spines on the rims becoming flattened towards their ends along their vertical axis. Specialised setae on the casings are nearly all white.

The specialised setae on the body are mostly of a pale, somewhat golden colour, the others being pure white or dark-coloured. Each side of a segment has some ten setae of ordinary form on the upper part of the ridge and many others in a mainly much lower position.

In captivity the larva spun webbing across a concave leaf or between two leaves, resting in the partially enclosed shelter thus formed. The duration of this instar was not determined. Length of larva at end of instar, when moderately extended and before contraction prior to moulting (*cf.* other larval measurements), about 5·5 mm.

Fourth Instar.

The spines on the tubercle-casing rims are now mostly of plain spiked type.

Duration of instar (one specimen), 48 days. Length of larva at end of instar, about 7·5 mm.

Fifth Instar.

Longitudinal medio-dorsal lines, at least in the case of some specimens, with dull vinous patches on some of the segments (these and the other

dull green longitudinal lines are initially more or less dull vinous coloured). A fifth, outer, longitudinal line is dull vinous-coloured. Neck-shield more or less dull vinous, with two rather amber-yellow areas posteriorly; anal-shield light, rather vinous, grey.

The honey-gland is situated as depicted in fig. 7. When functioning it bulges considerably. It can sometimes be induced to function and exude some of the liquid if the end of a hair is continually moved over the adjoining surface. (Excepting centrally, the dark areas in fig. 7 represent vinous-coloured markings.)

The tubercles (fig. 8) bend over strongly towards the gland when they are fully extended (everted) in order to allow the long hairs which extrude to reach the neighbourhood of the gland. The spines, pale yellowish brown in colour, on the casing-rim number approximately ten.

Spiracles (fig. 9) of a pale brownish colour with brown rings.

The setae of ordinary type (fig. 11) are nearly all pale-coloured, being somewhat darker at the ends of the body. The specialised setae, which are extremely numerous and partly produce the colour-effect in the larva, are represented in fig. 10. In some areas they are more star-shaped, whilst some have four projections and others six. Over most of the surface they are of a pale, somewhat golden colour, but on seg. I and the last few segments many are pure white. Some are golden-brown and a few are almost black.

Duration of instar (one specimen), 78 days. Length of larva at end of instar, about 10 mm.

Sixth Instar.

The ground-colour of the last few segments of a specimen examined was mainly pale grey-brown.

Duration of instar (one specimen), 107 days (26th June–11th October). Length of larva at end of instar, about 13 mm.

Final Instar.

The full-grown larva (figs. 12, 13, 15) is about 17 mm. in length. The body is markedly compressed, especially anally, as in previous instars; the first segment entirely covers the head when the larva is at rest.

Head (fig. 14) black, with the surface shiny; the lower section of the clypeus and an area on each side of it yellow-brown; division between lobes and a strip on each side of the clypeus pale grey; labrum orange-brown, its lower portion somewhat dull yellow and the skin above it pale grey; fleshy basal portion of antennae pale grey, the thick chitinised section more or less brown. The numerous pale, acuminate setae on the

lower part of the head, which extend further up on the front surface, are mostly very short; some of the lower ones are comparatively long and a number have a golden-brown tinge.

Body rather light green, partly slightly yellow-tinged. Ventral surface partly blue-green. The specialised setae are of the colours mentioned under the fifth instar and in places have a marked effect upon the pattern of the larva, especially white ones towards the anal end. Segment I is mainly brown-grey, rather vinous-tinged anteriorly. The neck-shield, large and somewhat circular in shape, has an extensive white area longitudinally across it, with white setae continuing from this portion on to the body anteriorly; elsewhere it is more or less grey, largely inclining to vinous, and posteriorly are two rather deep yellow patches. On the shield are some small dark depressions.

Longitudinal lines of a darker green than the ground-colour and not sharply defined. The medio-dorsal pair, fused on seg. II, are on the whole more distinct than the two sinuous lines on either side of them, and two other more laterally placed lines are less distinct than the latter. One specimen had the space between the medio-dorsal lines yellow. On seg. X there is some rather dull vinous colouring in a central posterior position, on XI is a patch of similar colouring in a central anterior position, its more posterior portion largely obscured by white setae, and on the inner side of each spiracle and extending up to each tubercle-casing is further colouring. Anterior to the anal-shield is a brownish-grey, curved transverse streak from which a central streak projects to the above-mentioned patch, and there is colouring on the outer part of the segment. Except where there is darker marking, the area between the tubercles is white or whitish, white setae occurring particularly densely here. Anal-shield whitish grey, grey anteriorly, with some small black depressions and bearing both light and dark setae. Around the shield are whitish areas and areas of light brownish or greenish grey, the contrast in colouring being largely due to the grouping of either light or dark setae: there is an outer darker area, on each side of the shield is a darker area extending posteriorly to the edge of the body, and behind the shield is a patch of darker colouring.

The honey-gland much resembles that in the fifth instar. The setae with projections have more projections, on the whole, than in the fifth instar.

The tubercles do not differ essentially from those of the fifth instar, as figured. One larva had eleven spines on one tubercle-casing rim and fourteen on the other. A small mite which found its way on to a larva caused the tubercles to function vigorously.

Spiracles more or less yellow-brown in colour with the rings dark brown. The spiracles are sunken, and those on segs. IV–X are small.

The setae of ordinary type are very numerous, and the main ones are comparatively long for a final instar *Phasis* larva. In addition to those on the ridge, fairly long setae, with shorter ones, occur in a lower position well below the ridge. With the exception of some of the smaller ones the setae are delicately barbed. They are mostly pale-coloured, but nearly all those at the anterior end of the body are more or less grey-brown, rather golden in certain lights. The specialised setae of the type depicted in fig. 10 usually have the projections rather more slender than in the figure, especially if the number is greater; on the main portion of the body the commonest number is six per seta; on a wide dorsal area on segs. X and XI the average number is appreciably greater. There are also some very short, relatively stout, plain setae, brown in colour, and many of them merely minute domed projections, which occur most noticeably on the yellow patches on the neck-shield. On the body there are a number of minute rings or slightly raised translucent protuberances with dark outlines.

Chitinised parts of the thoracic legs with a rich yellow-brown tinge, the extremities dark brown. The thoracic legs and the prolegs bear fine, light setae.

In the final instar and also at an earlier period the larva often eats the leaves of the food-plant along their edges as well as feeding on their flat surfaces, and the flowers also may be eaten. In captivity the larva fed during the daytime, generally for about half an hour at a time, with very long intervals of rest. Before pupating, a larva partially drew together, with a considerable amount of silk, the edges of a somewhat concave, upright leaf. It finally suspended itself by the anal-end to the inner surface of the leaf and pupated 4 days later. Duration of final instar (one specimen), 44 days.

Pupa.

The pupa (fig. 16) is 10·4 mm. in length and is fairly thick in proportion to its length. Front of pupa rounded; wing-bases rather protuberant; thorax convex dorsally, the prothoracic section medially depressed and bearing two protuberances; greatest width of pupa attained at about 0·7 of distance along wing-cases; abdomen begins curving downwards dorsally from the third segment and terminates obtusely.

The colouring of the mature pupa is as follows: Head-casing anteriorly, eye-cases partly, prothoracic section, mesothoracic section and part of metathoracic section above wing-cases very dark brown; prothoracic protuberances dull yellow to biscuit-coloured; wing-cases and the ventral portion between them more or less biscuit-coloured, the wing-cases with some brown colouring at the margins, especially the upper margins (*i.e.* upper

in the case of the pupa), and parts of the ventral portion between them brown; abdomen mainly orangy brown, darker in places (much darker posteriorly), and with some intersegmental portions orangy yellow; spiracles brown with a partial orange tinge.

Cremastoral hooks more or less ferruginous to golden-brown. Minute setae with broad serrated ends and somewhat similar to the larval setae are present on parts of the surface of the pupa. On the thorax, especially the prothorax, they have a definite lightening effect in some lights owing to their white colour. Also, on the prothoracic protuberances and in a small patch on each side of the seventh abdominal segment are minute, pale, branched setae.

The above description was made from a single pupa, which yielded a rather small male butterfly.

The abdomen of the pupa has a limited degree of flexibility. On one occasion when a pupa was touched, the portion of the abdomen beyond the fourth segment was seen to move with a rapid, almost trembling, motion. Pupal stage, 19 days.

Imago.

The imago (fig. 18, ♂ and ♀) is closely associated with the larval food-plants, upon which both sexes frequently settle, its flight not generally being rapid or of long duration. When at rest in the sunshine the wings are usually kept partly open, revealing the bright golden-orange colouring of the upper surface. The butterfly has been observed from the middle of September (though it probably appears earlier in the month) to late December, occasional specimens having been seen in January, but in some localities it does not seem to fly later than the earlier part of December. As far as can be judged, the insect is single-brooded. The rather lengthy flight-period of several months suggests that there might be a second brood, but, in view of the slow growth of the larva in captivity and the fact that, up to the present, only young larvae have been found on the food-plants in December, this is considered to be unlikely, normally, and the later appearance of some specimens is thought to be due to their having resulted from eggs laid late in the previous season or to retardation in the larval stage.

Distribution.

It has recently been ascertained that the insect has a very extensive range to the east of Cape Town, though there are as yet very wide gaps in its known distribution in that direction. Mr. A. J. H. Duke, of Cape Town, has shown me a male and a female specimen taken by himself on

the Bluff, Durban, on 27th October 1944 and 15th October 1943 respectively, which agree closely with examples from the Cape Peninsula. These specimens were flying about bushes of *Chrysanthemoides*.

Some localities in which the butterfly has been found within recent years are given below.

Western Cape Province.—Table Mountain (slopes); Lions Head (S.W. and W. slopes); Bachelors Cove; Camps Bay; Blinkwater Stream; Hottentots Huisie; nr. Llandudno; Kirstenbosch; Retreat; Muizenberg; St. James; Kalk Bay; Clovelly; Red Hill area, above Simon's Town; Strandfontein; southern end of Seven Weeks Poort (K. M. Pennington); Still Bay (D. A. Swanepoel).

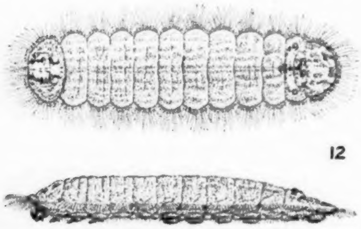
Eastern Cape Province.—Elands River, approximately 100 miles W. of Port Elizabeth (G. C. Clark).

Natal.—Bluff (S. side), Durban (A. J. H. Duke).

EXPLANATION OF FIGURES.

1. Egg (× 32). 2. Portion of side of egg (× about 160). 3. Larva two days after emergence (× 32). 3*a*. Larva: first instar, tubercle, right, extended (× about 75). 4. Larva: first instar, approximate cross-section (× 17). 5. Larva: first instar, head (× 90). 6. Larva: first instar, segment VII, left side (× 114). 7. Larva: fifth instar (at end of instar), small portion of seg. X with a smaller portion of following segment (× about 50), showing situation of honey-gland: its opening located beneath wide circular-headed setae across middle of figure. Intersegmental division expanded. 8. Larva: fifth instar, tubercle, right, partly extended, front view (× about 35). 9. Larva: fifth instar, spiracle, seg. V (× about 120). 10. Larva: fifth instar, small specialised setae, near lateral ridge (× about 110). 11. Larva: fifth instar, lateral setae on ridge (× 32). 12. Larva: final instar, before full growth (× 2·9). 13. Larva: final instar, approximate cross-section (× 1·24). 14. Larva: final instar, head (× approximately 10). 15. Larva: final instar, segment VII, left side (× 10). 16. Pupa, ♂ (× 2·72). 17. Food-plant: *Chrysanthemoides monilifera* (L.) T. Norl. (× 1). 18. Imago: ♂ and ♀ (× 1).

Habitat: Retreat, 7/11/33, and Muizenberg, 2/11/32 respectively.



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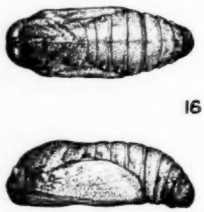

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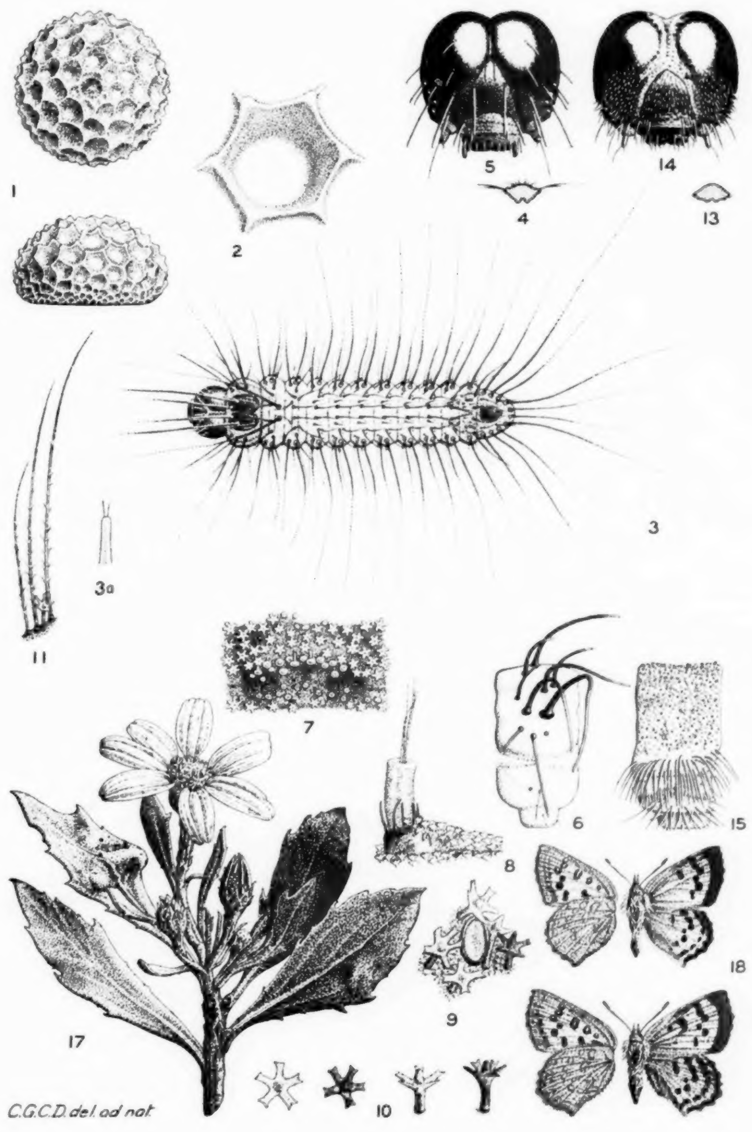

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THE GEOLOGY OF THE CANGO CAVES, OUDTSHOORN, C.P.

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(Read April 18, 1951.)

CONTENTS.

INTRODUCTION.

The Cango Caves are situated in the foothills south of the great Swartberg Range, some twenty miles from Oudtshoorn. They are easily reached by road and, being illuminated to reveal the full majesty of the great ornamental clusters of stalactites, are entered each year by many thousands of visitors.

The caves are a National Monument, with control vested in the Oudtshoorn Municipality, and to this body and its officers (especially Mr. Adams and Mr. du Plessis, the chief guide at the caves) our thanks are due for the privilege of studying freely within the caves. My companions were Mr. P. Matthews, M.Sc., F.G.S., and Mr. R. Clark, both of Natal University, and the work was aided by a grant for running expenses from the Council for Scientific and Industrial Research.

The Council desires to acknowledge the receipt of a grant from the University of Natal towards the cost of publication of this paper.

THE CAVE SYSTEM.

The system of caves is simple. The main chambers, visited on the tourist route, are arranged in tolerably straight sequence from the entrance westward, parallel to the strike of the country rock. They extend for a

distance of approximately a mile and a quarter. In this distance the maximum rise and fall of the path from the entrance level is only about 40 feet above and below. From the central route, subsidiary routes and chambers branch off, those on the south side frequently lower and those on the north frequently higher than the main route. Few of these chambers attain very large size, but many are of considerable interest in elucidation of the cave history.

For the narrative, a list of chambers in sequence along the tourist route is now given: entrance chamber, occupied by dressing rooms; first and second passages; van Zyl's Chamber, named after the discoverer of the caves; Louis Botha Chamber, with several smaller chambers to the south; passage; Rainbow Chamber; Bridal Chamber; passage; Fairy Chamber; Drum Chamber; Lot's Chamber (double); gallery; Lumbago Alley, with Crystal Palace to left at its far end; several passages with side chambers; the Japanese Umbrella; King Solomon's Mines; Chocolate Chamber, leading off to right at the top of the Iron Ladder; the Narrows; Ice Chamber; and Devil's Workshop, with the Devil's Chimney at the end. All these chambers occur in a single series; there is so far no evidence of further tiers of caverns at lower levels, though the possibility of such cannot be excluded.

The Environment of the Caves.

Both the solid geology and the surface history (geomorphology) of the district have exercised decisive control over the siting and mode of development of the caves.

As McIntyre has stated (1932, p. 81), the country rock in which the caves appear is a dark limestone. At some remote time the limestone was faulted and shattered along a zone which in places is at least 100 yards wide. The fissures made by this movement, in which shearing was prominent, were later sealed by deposition of calcite, making a mesh of white veins through the grey limestone, as can be admirably seen in the ceilings of many of the caverns. The vaulted ceiling of Louis Botha Chamber, in particular, has been rendered very beautiful by these effects.

Along this weakened zone underground water appears to have penetrated more freely, and hence the caverns have been excavated closely along this ancient line of fault. The dark limestone is, moreover (McIntyre, 1932), overlain by argillaceous schists, which have acted as an impermeable barrier to the passage of underground water from the Swartberg, forcing it to pass east and west through the limestone. Petrological factors have thus decided the east–west trend of the cave system.

The relation of the caves to the rest of the topography is no less important. On the north, the Swartberg soars to heights of six and seven

thousand feet. At the base of the range, and in the metamorphic rocks of the Cango Series, is a zone of foothills reaching in places up to 2300 feet above sea-level. The cave entrance appears at the 1800-foot contour, 100 feet above the bed of a small ravine tributary to the Cango River.

The foothills were formerly truncated by an erosion bevel, remnants of which may still be seen at intervals along the base of the Swartberg. In age, the bevel belongs to the "African" landscape cycle (King, 1949, p. 450). The significance of the former land-level in the formation of the caves is great, for their excavation was accomplished by subterranean agencies acting for a prolonged period beneath the plain. The Cango Caves are thus older than most of the landscape in which they appear, less old than the Swartberg but older than the ravine on which they debouch, older than the neighbouring valley of the Cango River and Schoeman's Poort, and older, in all probability, than the lowland of the Olifant's River Valley in which stands the town of Oudtshoorn. Their geological age is middle to late Tertiary.

These datings apply merely to the excavation of the caves, which were for long not visible; nor was there any ornamentation by stalactites, for the caves were still filled with water from floor to ceiling.

Then ensued a new stage in landscape-making. Following uplift of the subcontinent, the rivers of the region were enabled to incise their beds again. A small tributary from the Swartberg, rejuvenated in accordance with the trunk Cango River, then encountered the cave-level and broke open the entrance to the outer air. As the stream incised its valley further, below the cave-level, the water-table fell in sympathy and so the caves were drained. This stage, at which the caves were opened, may be dated provisionally as early Pleistocene.

This two-stage mode of development, involving a prolonged period during which the caves were tunnelled out beneath a relatively planed land-surface, and a later, briefer stage when valley excavation by rivers and streams acting in a new cycle of erosion exposed and drained the caves, is matched in all the various groups of Transvaal and Bechuanaland caves that I have examined in the past three years (King, 1951, p. 121), and seems, indeed, to be the normal mode of cave development in regions of soluble rocks (Davis, 1930, p. 450).

Excavation of the Caves by Vadose or by Phreatic Waters? *

Visitors generally believe that the caves were eroded out by an underground stream with a free-water surface and noticeable flow like a normal

* *Vadose* water is freely running like the water running into a bath; *phreatic* water permeates through a substance and moves only slowly like water held in a sponge.

stream above ground. But caverns of this type are more usually the result of phreatic waters filling permanently all the rock-spaces beneath the water-table and moving through the rock-host only with extreme slowness.

In the Cango Caves evidence on this point is conclusive: the caverns and passages were dissolved in the limestone by the passage of phreatic waters alone. Though, subsequently to the opening of the caves, flowing vadose water may temporarily have occupied parts of the cave system, their primary excavation was accomplished earlier (beneath the former water-table associated with the summit-bevel of the foothill region), before the descent of that water-table left them to dry out above it.

The evidence is as follows:

(*a*) There is no general fall in floor-level from the farthest recesses towards the entrance. Rather the level of the floor undulates, with broad low stretches in van Zyl's, Botha and Lot's Chambers. Subsidence of the floor into lower chambers is not admissible to explain these irregularities, nor are they due to falls of rock from the ceiling.

(*b*) Though the chambers become, in a very general way, larger towards the entrance there is no regular increase in size. The passages between the chambers are also irregular in size, and enter and leave the chambers at various heights above the floor.

(*c*) There are no erosional features visible on the floors, walls and ceilings that are attributable to stream abrasion.

(*d*) There are, on the contrary, one or two rock spans that reach from wall to wall of a chamber, making it in part two-storied. Such a span crosses above the entrance to King Solomon's Mines. Streams abrading downwards should leave no such spans bridging the passages they make.

(*e*) No deposits of sand or gravel *older than the main dripstone accumulations* have been found.

(*f*) The cave system, with many subsidiary chambers at lower and higher levels than the main line of caverns, could not be produced by stream abrasion, nor even by solution acting from the line of a normal vadose (free-surface) stream. Many subsidiary chambers project both "forward" and "backward" from the cross-cut passages which lead to them; and those with no outlet in either direction particularly could not be the work of a stream. In places, galleries run closely beside and below one another, intersecting irregularly to produce a maze or network of openings. Even where a gallery branches off from the main line of caverns and rejoins the line farther on, providing an alternative route (as, for example, the long gallery on the north side of Lot's Chamber), such double routes are not expectable features of either stream solution or stream abrasion.

All the features quoted under this heading are, on the contrary, typical and expectable where the whole body of the host rock was saturated with phreatic water able to dissolve material wherever it could circulate, however slowly, in crevices, galleries or caverns.

(*g*) Innumerable details of walls and ceilings, often with solutional pockets and with great corroded pendants of limestone (such as "the Heart, the Liver and the Lungs" which hang from the ceiling at the entrance to Lot's Chamber), show plainly that the caves were everywhere filled with water to the ceiling.

Enlargement of the caverns by rock-falls from the ceilings and walls has taken place at many stages. Rainbow and Bridal Chambers illustrate early collapses, while the caves were still full of water. Devil's Workshop displays, besides an early roof-fall, a talus of blocks without stalagmite which belongs to a new fall, while the roof is freshly broken and angular.

Internal Deposits of the Caves.

(a) *Red Clay.*

Throughout the caves, deposits of a uniform, unctuous red clay appear in favourable situations. The thickest deposits are at the beginning of Lot's Chamber and at the beginning of Lumbago Alley. These deposits are obviously secondary concentrations of clay derived from holes and pockets in the dark limestone or country rock, where it has been gathered through the long ages during which the plain summit-level was formed. Its original source was doubtless as insoluble impurity in the limestone at higher levels, carried down and concentrated until it filled all accessible cavities in the host.

Bretz (1942, pp. 681, 773) has discussed the occurrence of this red clay in limestone and dolomite cave systems at great length, and regards the "period of red clay-fill" as a typical stage in the development of such cave systems. The clay is considered to record very quiet water, in most cases up to the ceiling, making a completely filled subterranean reservoir. Only after the water and clay-fill episode are the caves drained. With his conclusions the Cango occurrences agree in every respect.

(b) *Dripstone.*

The stalactites and stalagmites for which the Cango Caves are justly famous are typical of such dripstone ornamentations in caverns the world over. Ideal conditions for the growth of stalactites seem, from observation,

to exist in wet caves with a liberal drip and a fairly free movement of air. Further, the distribution of several of the larger stalactite groups at Cango is also related to the occurrence of knots of calcite in the faulted zone of the roof.

Large stalactites and stalagmites are here not generally in a state of active growth; apparently they flourished when the quantity of water percolating into the caves was greater. Most South African caves are fairly dry at the present day and are acquiring only crystals and small stalactites as ornament. All the major dripstone formations are relics of an earlier, presumably wetter, régime.

The dripstone ornamentation of the inner chambers presents no abnormal feature, but the stalactites of several of the outer chambers experienced a reversal of conditions after the main stalactite groups were formed. Most of the stalactites and many of the stalagmites are not round and symmetrical like tree-trunks, but are narrow, fluted and bladed, and frequently so thin as to be translucent. Viewed in section across the broken ends, or on the sides, the growth-stages of the stalactites, marked by lines stained with red clay or iron oxide, do not approximate to circles or ovals but show only part of these sections like the grain on the end or face of a wooden plank. Thus only part of the normal growth appears in these stalactites, including the finest examples in the caves! * The stalactites obviously did not grow in that manner, but as the plank represents only part of a former round tree-trunk, so also these stalactites are only parts of former stouter columns, and their present relative fragility has been achieved only *by the dissolving away of much of the substance formerly composing the major groups*. In places, holes have been dissolved right through the fluted columns, and some are so thin that, though several feet in length, they may be bent to and fro with no great effort.

The episode of re-solution is of considerable interest in the history of the caves, but whether it occurred soon after the accumulation of the dripstone or much later is not known. A few instances show a thin deposit of newer limestone across the fluted surfaces, where it naturally appears unconformable to the earlier, truncated growth layers.

Minor dripstone formations, such as "baths" and "fans", "pool-collars" about stalactites and "splash-holes", may be seen at various points throughout the caves. They do not warrant special description.

Few crystal accumulations are to be seen along the tourist route, but in several of the side chambers off the inner caverns appear magnificent

* The older groups of stalactites are often stained a rich tawny orange which greatly enhances their appearance, but the more youthful display progressively less of this coloration. Evidently the depositing solutions brought less impurity from their passage through the roof as time went on.

crystalline displays. On the floor these usually build rosettes, an inch or so in diameter; on the roof they grow chiefly as pendants, terminating usually in a long rhombohedron combined with a long scalenohedron, and many show the double termination of twins. Repeated twinning is, indeed, very common, and apparently gives rise to those enigmatic curved forms called *helictites*, which are curiously abundant in the Cango Caves, *e.g.* in Crystal Palace.

Many of the smaller helictites and the more sharply curved parts of larger helictites show a remarkable uniformity of curvature, as though twinning occurred regularly and repeatedly, giving a closed or semi-closed ring. Helictites with a larger radius of curvature are generally less regular, and have parts of their length which even approximate to straightness as though twinning had for a time been suspended and then resumed.

There is, of course, no necessary regularity of twinning, as in one plane, and the corkscrew forms which result from changes in the plane of twinning are so precocious as to defy description. Good examples for study are provided in Chocolate Chamber, and on the Crown of Thorns, behind the Japanese Umbrella.

The growth of crystals upon the outsides of stalactites has sometimes thickened them considerably, converting them from slender pendants to thick, spiky clubs or glittering chandeliers.

Davis (1930, p. 622), recording a number of crystal-lined caverns in the United States, was of opinion that the crystals accumulated in the caves when they were refilled with water. But at Cango, and in the Transvaal caves, the crystals and helictites are always among the latest formations deposited. They grow upon the main dripstone and frequently appear alongside the most youthful stalactite tubes. Indeed, a general phase of crystal and small stalactite formation seems to be in progress, though the crystal grottoes are now moderately dry. We dissent, therefore, from Davis's opinion. Crystal growth takes place within a single drop of water equally with larger bodies, and indeed it is surprising how many of the crystal growth are tipped, to this day, with droplets of clear water.

(c) *Sands.*

Arenaceous deposits are seldon normal and appropriate deposits of cave systems. Silica present in the host limestone is usually fine grained, in the form of chert or flint, deposited perhaps from the colloidal state. The characteristic impurities of carbonate rocks are argillaceous, and we have already noted that red clay infills are the typical internal accumulations of caverns. Moreover, subterranean waters usually move with

extreme slowness, making their way through large and small spaces alternately so that anything like a noticeable current is absent.

It follows, therefore, that sand deposits, where they do occur within cave systems, are of special significance and have frequently been introduced from outside by entering waters. These considerations lend a special interest to the arenaceous deposits within the Cango Caves. They are few in number and may be studied *seriatim* from the entrance.

(*a*) At the cave mouth, before the area was blasted to make a site for the power-house, was a set of cave-mouth breccias and sands like the breccias and sands at the mouths of Transvaal caves which have yielded the bones of many creatures, including man-like apes. Of the Cango occurrence little remains. The sands, from samples which I was able to collect down the hill-slope, seem to belong to two groups, the former of which, finer in texture, was cemented and broken into pieces before being included in the latter, which is a bone-breccia like the famous bone breccias of Sterkfontein and Makapansgat.

Some of the minerals are from the limestone, others from the Table Mountain sandstone, and there is a wide range of minerals from various schists. In the samples examined are no typically wind-blown grains of quartz.

(*b*) Dust from the floor within the cave entrance contains a heterogeneous assemblage of minerals, much having doubtless been introduced upon the feet of tourists.

(*c*) In the passage before van Zyl's Chamber are two series of sands, one lying on the other. The lower sand, crudely stratified, is medium to coarse grained, angular to sub-rounded. The minerals are quartz, feldspar, garnet, rutile, zircon. Many of the smaller heavy grains are very worn and may have come from the limestone, but the bulk of the deposit is an introduced sand derived from the Table Mountain sandstone of the Swartberg.

The overlying sands are of special interest, for standing vertically in them is the jawbone of one of the larger species of buck. This is the only sand in the Cango Caves that is very calcareous. Like the sand below, it contains two contrasted portions of indigenous and of extraneous derivation.

(*d*) Bedded siliceous sand from along the path between van Zyl's and Louis Botha Chambers is mostly fine-grained sintery silica, indigenous to the Cango Series. It is free from impurities other than small cubes of limonite pseudomorphous after pyrite, and local additions, in the upper part, of typical quartroze grains of Table Mountain sandstone which have possibly been introduced artificially. At its densest, the material becomes a fireclay.

(*e*) At the beginning of the descent into Lot's Chamber appear characteristically fine-grained sands containing quartz, mostly subangular, euhedral

magnetite, ilmenite and zircon, with subhedral hornblende, garnet and muscovite. This sand is strictly of local derivation, the minerals coming, doubtless, from streaks of argillaceous schist traversing the Cango limestone.

(*f*) A red sand with clay from the beginning of Lumbago Alley consists of fine to medium poorly graded quartz sand. The grains are all angular but none euhedral. The heavy minerals are much finer still, and include limonite, hematite, magnetite, zircon, feldspar, garnet, ? dolomite, galena and fluorite with a micaceous mineral, all of them angular or euhedral. These have been derived from the limestone or from dolomitic and schistose lenses.

The sands thus fall into two classes: those wholly of internal derivation, and sands whose grains have been partly derived from outside, and in particular from the Table Mountain sandstone of the Swartberg. But even in these latter are none of the characteristically wind-worn quartz grains so conspicuous in the cave sands of the Transvaal and which were derived during periods of relative aridity when Kalahari climatic conditions extended farther to the east. Such conditions evidently did not reach to the Cango region south of the Swartberg.

The Later History of the Caves.

After the descent of the water-table the caverns were no longer filled with ground-water, but rain-water, percolating through the roof and dripping from the ceilings and walls, then made the various dripstone masses that now so richly ornament the caves. The rate of deposition of this material seems to have been fairly rapid and to have been synchronous throughout the caves. As a general rule, the largest stalactites occur in the largest chambers, and these are nearest the entrance, suggesting that the rate of drip was greater where the roof was thinner.

The episode following the main dripstone, when many of the main groups were largely dissolved away again, is important in the cave history, for it may well have been at this time that the extraneous sand deposits which reach into the first few chambers were introduced. The effects of re-solution do not extend back far beyond Louis Botha Chamber—a distribution matched by that of the extraneous sands—showing that the hinder chambers were then sealed off. They appear not wholly to have escaped inundation, however, for several of the farthest chambers show crusts of pool-surface deposition ringing their earlier stalactites. The whole episode of inundation and introduction of foreign sands is, notwithstanding, difficult to explain and date.

Such an event is not usual in the straightforward development of limestone caverns, and involves a reversal of processes which have hitherto

resulted in deposition. Appeal may be made to forces either internal or external to the cave system, and both seem capable of producing re-solution of earlier dripstone. Thus in the first case, as the roof thinned under subaerial erosion, and rain-water charged with carbon dioxide percolated more abundantly to the outer caves, dissolving little or no calcite from the limestone roof on the way, it could re-dissolve the dripstone masses which had been constructed earlier by the same agency. Herein is no violation of the normal cycle of cavern development, but the hypothesis fails to account for the introduction of foreign sands and the absence of a smooth stalagmite floor. Details of the re-solution, too, sometimes suggest that it was accomplished, not by thin films of drip-water running down the stalactites, but under-water which filled the outer caves entirely. That this water introduced the foreign sands seems a reasonable assumption; but the manner of the inundation remains obscure if the level of the outside stream had previously fallen below the outlet to allow the drying out and ornamentation of these caverns.

The possibility cannot be excluded that the passage leading to van Zyl's Chamber, where the sands have been cut through to enlarge the entrance, was formerly completely blocked, thus permitting the chambers behind to fill with rain-water which had percolated through the roof. Alternatively, the cave may at one time have had an outlet through the roof, but exploration is yet insufficient to establish this. The stalactites immediately on the right of the entrance to van Zyl's Chamber lead, indeed, to a small passage along the ceiling, and although this does not appear to extend far, others may do so.

Climatic changes, well known elsewhere in South Africa during Pleistocene time, may also have played a part in this reversal of the normal order of cave evolution, but they are difficult to evaluate here. For comparison, we may note that above the underground lake at Sterkfontein the dripstone roof has been re-dissolved in part, thus showing that this lake filled the cavern to the roof subsequently to the deposition of the main dripstone there.

Ultimately the very wet phase passed from the outer chambers, and the inner chambers connected up along the general line to give a system of caverns essentially that of the present day.

Nowadays, a renewed deposition of dripstone and a growth of crystals are taking place at intervals in the smaller caverns. Thus, in the chambers left of the Pulpit small stalactites broken by early visitors (the earliest date I have noticed scrawled upon the walls is 1817) are being repaired or lavishly reformed. In the Crystal Palace the roof and floor are adorned with a most lovely growth of calcite crystals, including helictites.

Though the dispersal of the cave-mouth breccias without record of their fossil contents is a permanent loss, the sharp eyes of M. l'Abbe H. Breuil

have discovered two rock-paintings of an elephant (in red clay and black) and a kudu (black), and his excavations in the second side gallery recovered Stone Age implements. These are the only records of prehistoric human occupation.

Comparisons with Transvaal Caves.

One of the chief objects of this research was to ascertain in how far the history of the caves at Cango corresponded with events already recorded at a number of cave sites in the Transvaal (King, 1951, p. 121 *et seq.*).

These events may briefly be rehearsed.

The Transvaal dolomite caves developed along shatter-zones which had been re-cemented with calcite. They were developed phreatically, and were drained following incision of neighbouring surface streams in a new cycle of erosion.

Outside the caves a red sand was being blown about by the wind, and this blew into the outermost caverns as they were opened. From these sands at Sterkfontein and Makapansgat come the various Australopithecine races—*Australopithecus, Plesianthropus* and *Paranthropus.*

The phase of the older red sand was succeeded by that of the main dripstone when the caves received their main stalactites and stalagmites. This dripstone almost everywhere cemented the older red sand deposits. The period seems to have been prolonged.

Following the dripstone in the Transvaal caves is a second incursion of red sand of Kalahari type which at Makapan is two-phase. The earlier sub-phase contains late Chelles-Acheul implements, and the later a Middle Stone Age assemblage. The latest episode in the Transvaal caves has been a growth of small stalactites and crystals.

The correlation of the various Transvaal caves, effected not only by normal features of the cavern cycle but also by incursions of foreign material and reversals of spelean sequence repeated from cave to cave over a wide area, has a high degree of probability.

Minor differences appear, of course, in the dates of opening of the caves; thus the Sterkfontein Caves were opened *before* the accumulation of the older (Australopithecine) red sand, whereas the Makapan Caves were opened *during* the period of accumulation of this sand. The Lobatsi Caves in Bechuanaland had no deposits of the older red sand—their deposits began with the main dripstone era—while Mwulu's Cave near Pietersburg, described by Tobias, has as its oldest spelean deposit the newer red sand of the Middle Stone Age.

It remains now to attempt a correlation of the situation, origin and history of the Cango Caves with those of the Transvaal.

The situation of the Cango Caves in the side of a narrow ravine resembles most the setting of the Cave of Hearths at Makapan, though the opening of the Cango Caves is probably somewhat younger. From this starting-point we may tentatively correlate the main dripstone deposits in each. The growth of dripstone is in itself independent of geological age, but it may be a function of (*a*) stage of development in the cavern cycle, when caves opened at different epochs may show morphological similarity though they are not coeval, or (*b*) climatic regimen, when the formations, if in districts under similar climatic controls, are coeval though the caverns themselves may be of different age. The heavy dripstone phase of Cango may therefore not be wholly due to draining of the caves in the cavern cycle (morphological), but may also have climatic significance, correlatable with conditions in the Transvaal.

As we have noted, the cave-mouth breccias at Cango were destroyed. Nevertheless, the slender evidence afforded by loose fragments lying on the hillside below suggests a two-phase deposition of these materials like the two phases of the newer red sand at Makapan. The situation of the red sand-breccias on the threshold of the existing caves is also similar to that at Makapan, and the two deposits may well be deemed to be of the same age. The irruptions of sand (derived from the Table Mountain sandstone) into the Cango Caves may be of this same age, or later, as also the period of re-solution of the main stalactite groups.

The latest deposits—small stalactites, helictites and crystal growths—are common to the Cango as well as to all the Transvaal caves and afford a last point of similarity.

Four congruous points of situation and spelean sequence have thus been adduced in support of a correlation between the Cango and the Transvaal caves. Probably these are sufficient to indicate a parallel development in the two areas, though, as we have noted earlier, the wind-blown sands of Kalahari type so abundant in the cave-deposits of the Transvaal do not appear at Cango.

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CONTRIBUTION À LA CONNAISSANCE DES HOLOTHURIES DE L'AFRIQUE DU SUD.

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LISTE DES ESPÈCES ÉTUDIÉES.

EXPLICATION DES SYMBOLES INDIQUANT L'ORIGINE DES SPÉCIMENS ENVOYÉS PAR L'UNIVERSITÉ DE CAPE TOWN.

AFR.—Survey Vessel Africana.
AR. 7C.—Arniston.
BR. 1E.—Buffel's River.
CH. 5F.—Cape Hangklip.
FB.—False Bay.
KNY.—Knysna Estuary.
LB.—Langebaan Lagoon.
SB.—Saldanha Bay.
TB.—Table Bay.
U. 10J.—Umhlali.
W. 10B.—Port-Edward.
YZ. 4D.—Yserfontein.

Monsieur le Professeur J. Day, auquel j'adresse tous mes remerciements, a bien voulu me faire parvenir, pour étude, un certain nombre d'Holothuries récoltées en différents points des côtes Sud-Africaines ou au large de celles-ci, depuis Port-Nolloth jusqu'à Delagoa Bay. Par ailleurs, le Muséum de Paris possède une petite collection d'Holothuries du Cap de Bonne-Espérance. Grâce à ce matériel, il m'a été possible de préciser quelques points intéressants concernant certaines espèces, notamment *Cucumaria sykion* Lampert et *Cucumaria insolens* Théel, et de décrire huit espèces nouvelles pour la Science, ce qui porte à trente neuf les espèces actuellement connues de l'Afrique du Sud.

Il est curieux de constater que ce n'est qu'à une époque relativement récente que les Echinodermes sud-africains ont été étudiés dans leur ensemble. Ils ne furent longtemps connus que par des travaux fragmentaires très échelonnés dans le temps. La première Holothurie décrite le fut, en 1766, par Pallas, sous le nom de *Actinia doliolum.* Puis vinrent Quoy et Gaimard, 1833, avec *Holothuria aurea*; Ludwig, 1874 (*Cucumaria improvisa*) et 1882 (*Cucumaria frauenfeldi*); Lampert, 1885 (*Holothuria parva, Cucumaria posthuma, Cucumaria Jägeri, Semperia sykion*); Théel, 1886 (*Cucumaria insolens, Cucumaria capensis, Cucumaria discolor*); Vaney, 1908 (*Thyone articulata*); Britten, 1910 (*Cucumaria leonina* var. *africana, Thyone serratus*).

Il faut attendre 1923 pour qu'une étude d'ensemble des Echinodermes de l'Afrique du Sud, y compris les Holothuries, soit faite par H. L. Clark, qui décrit trois formes nouvelles: *Holothuria grammata, Cucumaria spyridophora, Psolus imperfectus.* Ensuite, quelques auteurs ont précisé les caractères de formes connues ou décrit des espèces nouvelles pour la Science:

Heding, 1929 (*Patinapta crosslandi*), 1937 (*Rhopalodinopsis capensis*), et 1938 (*Cucumaria tetracentriophora*); Ludwig et Heding, 1935 (*Pentamera chuni, Pentamera velligera, Thyone venustella, Cucumella triplex, Psolus capensis, Psolus agulhasicus*); D. John, 1939 (*Cucumaria stephensoni*); Deichmann, 1944 (*Urodemas bifurcatum*).

Dans son excellente révision des Holothuries de l'Afrique du Sud, parue en 1948, Miss E. Deichmann, en plus des espèces citées plus haut et dont les exemplaires types ont été récoltés sur les côtes sud-africaines ou au large de celles-ci, rapporte à des espèces vivant ordinairement en Mer rouge, mais aussi aux Iles Hawaii et aux Iles Marshall, des spécimens provenant des côtes est d'Afrique. Il ne semble faire aucun doute que *Urodemas ehrenbergii* Selenka et *Cucumaria crucifera* Semper, de la Mer rouge, ainsi que *Afrocucumis africana* (Semper), de Querimba, existent bien jusqu'au sud de Durban. Par contre, il est très douteux que les Aspidochirotes, récoltées également au sud de Durban, appartiennent les unes à *Holothuria cinerascens* (Brandt) (Localité type: Ile Bonin), les autres à *Holothuria leucospilota* (Brandt) (Localité type: Ualan). N'ayant pas les exemplaires sous la main, je ne puis me prononcer d'une façon certaine. Mon doute provient de ce que Miss Deichmann considère comme identique à *Holothuria leucospilota, Holothuria fusco-rubra* Théel, des Iles Hawaii, et *Holothuria vagabunda* Selenka, des Iles Hawaii et des Iles de la Société. Or, dans un travail actuellement en cours de publication, je constate que *H. fusco-rubra* est une espèce bien distincte de *H. vagabunda des auteurs*, qui n'est peut-être pas *H. vagabunda* Selenka—pour autant que les exemplaires types des Iles Hawaii soient identiques aux exemplaires types des Iles de la Société—. Quant à savoir ce qu'est exactement *H. leucospilota*, il faudra attendre que soit réexaminé le type de Brandt, s'il n'est pas perdu.

Il me faut dire aussi quelques mots sur la contreverse qui s'est élevée entre Miss Deichmann et T. A. Stephenson au sujet de *Cucumaria sykion* et de *Cucumaria insolens*. Miss Deichmann pense que les Holothuries trouvées sur la côte ouest, du Cap des Aiguilles à Port-Nolloth, et rapportées à *C. insolens*, ne sont que des formes immatures de *C. sykion*, dont l'aire de répartition s'étend du Cap des Aiguilles au nord de Durban. De son côté, T. A. Stephenson s'étonne de cette assimilation, la couleur des animaux vivants, leur taille, leur mode de vie éloignant nettement l'espèce d'eau froide *C. insolens*, de l'espèce d'eau chaude *C. sykion*. Miss Deichmann appuie ses dires sur une évolution des spicules à l'intérieur de l'espèce, suivant l'âge de l'animal: les spicules des jeunes *insolens* et des jeunes *sykion* seraient identiques, alors qu'ils deviendraient dissemblables chez l'adulte. Je n'entreprendrai pas ici une discussion sur la soi-disant transformation des spicules, ce qui nous entrainerait fort loin. Je me bornerai à souligner que l'on a souvent confondu formes jeunes et espèces de petite

taille; s'il est vrai que les spicules des premiers stades de croissance de l'animal sont souvent différents de ceux de l'adulte, il n'a jamais été prouvé que les spicules de l'animal définitivement constitué ne ressemblent en rien à ceux du même animal arrivé à maturité; bien au contraire, à de très rares exceptions près qu'il serait bon de vérifier, on retrouve toujours chez l'adulte, au moins dans la région anale, notamment pour les Dendrochirotes, les spicules typiques des immatures.

J'ai pu examiner un grand nombre de *C. insolens* et seulement deux exemplaires de *C. sykion*. Cependant, mon avis est formel: *C. insolens* et *C. sykion* sont deux espèces absolument distinctes; bien mieux, il existe une troisième espèce, que j'ai nommée *Cucumaria sinorbis*, dont l'aire de répartition s'étend de Tabel Bay à Port-Edward. *Cucumaria insolens* n'est pas une forme immature de *C. sykion*; c'est une espèce de petite taille; elle incube ses jeunes dans des poches dorsales, comme le font de nombreux dendrochirotes antarctiques; il s'agit donc bien d'une espèce d'eau froide. Par contre, *C. sykion*, espèce d'eau chaude, n'est pas incubatrice, pas plus que *C. sinorbis*. Les trois espèces se distinguent aisément par leur morphologie, leur anatomie et la forme de leurs spicules. Un tableau, accompagnant la description de ces trois espèces, met en relief les points principaux qui permettent de les distinguer.

Comme je l'ai dit plus haut, je décris dans ce travail huit espèces nouvelles pour la Science: deux Synallactes, trois Cucumaria, une Thyone et deux Synaptes. Ce qui frappe le plus lorsque l'on examine la liste des Holothuries d'Afrique du Sud, c'est la pauvreté en Aspidochirotes et en Apodes. Il est vraisemblable que des recherches plus poussées permettront de découvrir de nouveaux documents, surtout en Apodes.

HOLOTHURIOIDEA Bronn

Ordre ASPIDOCHIROTA Grube, 1840.

Tentacules peltés, généralement au nombre de vingt, rarement de vingt-cinq ou trente, constitués par une tige courte se terminant par un disque élargi, plus ou moins couvert de petites digitations. Pas de muscles rétracteurs du pharynx. Appendices ambulacraires pouvant être soit des pieds, soit des papilles ou les deux à la fois sur le même animal. Organes arborescents bien développés. Ampoules tentaculaires généralement présentes dans les formes littorales, manquant dans les formes d'eau profonde. Tubes de Cuvier absents, peu développés ou extrêmement abondants. Canal hydrophore s'ouvrant ou non à l'extérieur. Gonades en une ou deux touffes. Le mésentère appartenant à la troisième boucle de l'intestin tourne dans l'interradius ventral droit. Les spicules, quand

ils existent, se présentent, seuls ou mélangés, sous forme de corpuscules crépus, de baguettes pointues, de corpuscules en C ou de tourelles plus ou moins développées.

FAMILLE SYNALLACTIDAE Ludwig, 1894.

Corps rarement cylindrique, généralement aplati et présentant souvent une sole ventrale portant des pieds ambulacraires alors que la surface dorsale porte des papilles. Pas d'ampoules tentaculaires. Un seul canal hydrophore dont l'extrémité distale est en relation avec la paroi du corps. Muscles radiaires généralement indivis. Deux organes arborescents. Pas d'organes de Cuvier. Spicules: Tourelles, parfois des corpuscules en C, très rarement des boutons.

Genre SYNALLACTES Ludwig, 1894.

Corps cylindrique ou subcylindrique. Dix-huit à vingt tentacules. Pas d'ampoules tentaculaires. Canal hydrophore rattaché à la paroi du corps. Face ventrale aplatie mais non limitée par un rebord marginal; pieds ambulacraires répartis suivant les radius sur une ou plusieurs lignes. Face dorsale possèdant des papilles disposées en séries linéaires. Deux buissons de tubes génitaux, placés de part et d'autre du mésentère dorsal. Anus non logé dans un sillon et dépourvu de dents calcaires. Muscles radiaires divisés en deux rubans. Corpuscules calcaires de la peau consistant souvent en sclérites cruciformes portant en leur centre une longue tige simple, bifide ou trifide au sommet; toujours des bâtonnets dans les appendices ambulacraires. Couronne calcaire massive, sans prolongements postérieurs.

Synallactes viridilimus n. sp.

Pl. *35*, figs. 1–17; pl. *36*, figs. 16–17.

Spécimens étudiés.

Université de Cape Town: AFR. 700 C., 1 ex. récolté le 19–V–1947 par 32° 33′ S.—16° 31′ E. et 290 fth. de profondeur; fond de vase verte.

L'unique exemplaire, très contracté et à tentacules invaginés, mesure environ 145 mm. de long sur 35 mm. dans la plus grande largeur. Le corps est subcylindrique, légèrement aplati ventralement. Le tégument lisse, très épais, est violet foncé dorsalement, gris violacé sur le ventre.

Les pieds ventraux, violacés, sont longs, cylindriques, terminés par une large ventouse soutenue par un énorme disque calcaire très réticulé, portant presque toujours un réseau secondaire pouvant prendre un grand développe-

ment. Les pieds sont très nombreux et serrés, disposés sur deux rangs le long des radius latéraux, sur quatre rangs le long du radius médian.

Les papilles du bivium sont longues, coniques, grisâtres, assez nombreuses mais espacées et disposées apparemment sur cinq–six rangs longitudinaux à intervalles réguliers; il n'est pas possible, vu l'état de contraction du corps, de dire si ces rangées sont limitées aux radius; cependant, à la limite du trivium, les papilles deviennent bien plus longues et forment une rangée bien distincte.

Bouche et anus ventraux. Vingt tentacules jaunâtres, grands, disposés sur deux cercles: un cercle interne possédant sept tentacules, un cercle externe en comprenant treize. La couronne calcaire (*36*, 17) est peu calcifiée, enrobée dans une membrane et sa forme est difficile à saisir. Deux longues vésicules de Poli, situées ventralement, plissées, rubanées, de couleur violet très clair. Un petit canal hydrophore. Estomac musculeux. Muscles longitudinaux très larges, épais, séparés par un profond sillon sur le premier tiers antérieur, minces et ne portant plus qu'un sillon à peine visible sur le reste de leur parcours. Gonades formées d'un grand nombre de tubes très longs, très ramifiés, emplissant presque toute la cavité générale. Papille génitale bien développée, conique, située dorsalement à l'intérieur du cercle tentaculaire externe. Petit cloaque.

Spicules.—Les pieds ventraux sont soutenus par de grands bâtonnets très minces, à extrémités à peine élargies et plusieurs fois perforées, et dont le corps proprement dit porte de fortes épines irrégulièrement distribuées (*36*, 16). Il existe aussi, mais en bien moins grand nombre, des bâtonnets plus épais, portant sur un seul de leur côté et sur toute leur longueur de longues ramifications pouvant s'anastomoser pour former un réseau à une ou plusieurs grandes mailles accompagnées de petits trous marginaux.

Les bâtonnets des papilles dorsales sont identiques à ceux des pieds ventraux.

Le tégument ventral est bourré de tourelles dont la base est formée le plus souvent de trois à cinq branches non perforées (*35*, 12, 17) ou percées chacune d'un grand trou terminal (*35*, 15, 16); la flèche est assez haute et se termine par trois pointes (*35*, 16); les branches de la base peuvent se réunir pour former un véritable disque (*35*, 9) mais les spicules ainsi construits sont rares. On trouve aussi de très petites tourelles à disque étroit, dont la flèche est formée de deux, trois ou quatre piliers, ajourés ou non au sommet et armés d'une ou plusieurs aspérités latérales (*35*, 7, 8 11).

Le tégument dorsal possède les mêmes spicules que le tégument ventral, à l'exclusion des petites tourelles à disque étroit, mais avec, en plus, de nombreuses tourelles bien plus grandes dont la base a trois bras simples (*35*, 4) ou ramifiés (*35*, 3) qui peuvent se réunir pour former un disque presque complet (*35*, 1); la flèche est haute (*35*, 6), percée ou non d'un trou près du

sommet (*35*, 5). On trouve également des tourelles dont les bras sont bien plus grêles (*35*, 10, 14).

Les bâtonnets des tentacules, de tailles diverses, sont le plus souvent imperforés ou avec un seul trou à l'une des extrémités; ils sont droits (*35*, 2) ou incurvés (*35*, 13), toujours épineux.

Rapports et différences.—Synallactes viridilimus se rapproche de *Synallactes challengeri* (Théel), récolté aux approches des Iles Crozet, par la forme du corps, la disposition des pieds et des papilles, ainsi que par la forme des petites tourelles du tégument ventral. Par contre, *S. challengeri* ne possède pas de tourelles à véritables flèches à trois ou quatre piliers, ni les grandes tourelles à large disque comme celles que l'on rencontre dans le tégument dorsal de *S. viridilimus*.

Synallactes mollis n. sp.

Pl. *36*, figs. 1–15, 18, 19.

Spécimens étudiés.

Université de Cape Town: AFR. 723.V.7B, 1 ex. récolté le 10–VIII–1947 par 31° 30′ S.—17° E. et 200 fth. de profondeur.

L'unique exemplaire, bien étalé, extrêmement mou, mesure environ 220 mm. de long sur 50 mm. de large; il est nettement aplati ventralement. Le tégulent, d'environ 1 mm. d'épaisseur, est violet sur le dos, gris jaunâtre sur le ventre. La bouche est subventrale, l'anus terminal. Il y a dix-huit tentacules répartis sur deux cercles: dix tentacules externes assez petits, gris jaunâtre, et huit tentacules internes dont deux identiques à ceux du cercle externe et six réduits à l'état de moignon.

Les pieds du trivium, longs, cylindriques, blanchâtres, sont terminés par une large ventouse soutenue par un énorme disque calcaire; ils sont disposés sur deux rangs le long des radius latéraux, sur 4–6 rangs le long du radius médian.

Les papilles du bivium mesurent jusqu'à 15 mm. de long, sont coniques, violacées à la base, jaunâtres au sommet; elles sont peu nombreuses et disposées sur six rangées longitudinales également espacées, réparties sur les radius et les interradius.

La couronne calcaire (*36*, 19) est bien calcifiée, massive, de forme très irrégulière, et l'on ne distingue les radiales des interradiales que par l'empreinte des muscles. Deux vésicules de Poli. Un canal hydrophore. Muscles longitudinaux larges, minces, non divisés par un sillon. Poumons en deux longues touffes très ramifiées, violet foncé, atteignant la moitié de la longueur du corps et débouchant dans un petit cloaque par un long canal commun.

Spicules.—Les bâtonnets des pieds ventraux sont assez grêles, toujours épineux, à extrémités à peine élargies le plus souvent imperforées mais percées parfois d'un ou deux petits trous; de tailles très diverses, ils sont droits ou incurvés (*36*, 18).

Les bâtonnets des papilles dorsales sont identiques à ceux des pieds ventraux, mais bien moins nombreux.

Dans le tégument ventral, on trouve deux sortes de tourelles. De très petites à base étroite formée de trois à quatre bras perforés aux extrémités, surmontée d'une haute flèche terminée par trois pointes, imperforée (*36*, 5, 6, 12) ou percée d'un petit trou près du sommet (*36*, 1); cette flèche est toujours simple et il n'y a pas d'esquisse de formation de piliers. Des tourelles bien plus grandes, à base formée de trois ou quatre bras à extrémités élargies et percées d'un grand trou central et d'un ou plusieurs petits trous périphériques (*36*, 3, 10, 13); cette base est surmontée d'une haute flèche simple terminée par trois fortes pointes, imperforée ou le plus souvent percée d'un grand trou près de l'extrémité (*36*, 8, 10, 13).

Le tégument dorsal n'a pas de petites tourelles mais uniquement de grandes tourelles, généralement à trois branches (*36*, 2, 7, 14), parfois à quatre branches (*36*, 4, 9) et dont la flèche est identique à celle des tourelles du tégument ventral; ces tourelles sont bien moins nombreuses mais plus grandes que celles du tégument ventral; les bras de la base ne se referment jamais pour former un disque plus ou moins régulier, comme cela à lieu pour *S. viridilimus*.

La région anale, en plus des divers spicules énumérés ci-dessus, possède de grandes plaques épaisses très réticulées.

Les bâtonnets des tentacules sont très nombreux, de taille très variable, toujours à bords épineux, droits (*36*, 11) ou fortement incurvés (*36*, 15), imperforés ou ne portant qu'un très petit trou à une ou aux deux extrémités, qui ne sont pas élargies.

Rapports et différences.—*S. mollis* se rapproche de *S. viridilimus* par la disposition de ses tentacules, celle des pieds ventraux et des papilles dorsales. Les tourelles rappellent, par leur base, celles trouvées chez *Synallactes crucifera* Perrier, des côtes du Maroc, mais la flèche en est totalement différente.

Ordre DENDROCHIROTA Grube, 1840.

Pieds répartis selon les radius ou envahissant plus ou moins les interradius. Tentacules ramifiés, au nombre de dix à trente. Ampoules tentaculaires le plus souvent absentes, parfois présentes mais très réduites. Muscles rétracteurs présents. Deux organes arborescents, parfois reliés à l'intestin. Un ou plusieurs canaux hydrophores situés dans la cavité égnérale. Une ou plusieurs vésicules de Poli. Mésentère de la boucle

intestinale inférieure situé à gauche ou à droite de l'interradius ventral. Le plus souvent, pas d'organes de Cuvier. Spicules du tégument de formes très variées: grandes plaques lisses, boutons noduleux se transformant en grandes plaques noduleuses dont une extrémité est souvent amincie et épineuse, corpuscules en cône de sapin, délicates corbeilles, ellipses fenestrées, tourelles, baguettes ramifiées ou non.

Famille CUCUMARIIDAE R. Perrier, 1902.

Corps plus ou moins cylindrique ou fusiforme, parfois fortement incurvé; pas de sole ventrale nettement définie. Dix tentacules. Pieds limités aux radius ou également dispersés sur les interradius. Mésentère de la boucle intestinale postérieure à gauche de l'interradius ventral.

Genre Cucumaria Blainville, 1830.

Dix tentacules de taille égale ou dont les deux ventromédians sont plus ou moins réduits. Bouche et anus terminaux. Pieds disposés en bandes longitudinales sur les radius, parfois dispersés sur les interradius, surtout sur la face dorsale. Couronne calcaire composée de dix pièces sans prolongements postérieurs. Spicules: plaques et boutons, lisses ou noduleux; présence ou non de corbeilles délicates; plaques périproctales souvent présentes, parfois de véritables dents anales.

Cucumaria frauenfeldi Ludwig

Pl. 37, figs. 1–14.

? *Cucumaria* sp. Semper, 1867, p. 236, pl. xxxix, fig. 22.
Cucumaria frauenfeldi Ludwig, 1882, p. 130.—Théel, 1885, p. 109.—Ludwig, 1887, p. 1231.—Britten, 1910, p. 239.—H. L. Clark, 1923, p. 413 (partim).—Hogben et Van den Lingen, 1928, p. 292.—D. John, 1939, p. 325.—Deichmann, 1948, p. 345, pl. xviii, figs. 13–17.
Cucumaria posthuma Lampert, 1885, p. 248.—Théel, 1885, p. 265.

Spécimens étudiés.

Museum de Paris: Cap de Bonne Espérance, M. Delalande, 1820, 2 ex. étiquetés *Pentacta crumena* Valenciennes (nom jamais publié).

Les deux échantillons ont dix tentacules bien étalés, de taille égale, de couleur noirâtre. Le corps est fortement incurvé, le bivium étant nettement raccourci par rapport au trivium, qui est fortement renflé; de ce fait, l'anus est dorsal alors que la bouche est nettement subdorsale. Le plus grand exemplaire mesure 44 mm. de la bouche à l'anus par le bivium et 72 mm. par le trivium; la largeur et la hauteur sont égales: 32 mm. Le tégument, lisse, épais, est marron très foncé à noirâtre sur le dos, marron très clair sur le ventre.

Les pieds sont identiques sur tous les radius, quoiqu'un peu moins nombreux sur ceux du bivium; ce sont des appendices noirâtres, courts, cylindriques, terminés par une ventouse soutenue par un petit disque calcaire chez les pieds ventraux; ils sont répartis sur deux rangs aux extrémités, sur trois-cinq rangs au milieu du corps; il n'y a pas de papilles interradiaires.

Le mauvais état de conservation de mes échantillons ne me permet pas de préciser l'organisation interne dont, seule, la couronne calcaire est bien conservée; celle-ci se compose de radiales subtriangulaires à extrémité antérieure à pointe mousse, à bord postérieur ondulé, et d'interradiales bien plus petites, très larges, unies aux radiales par un segment calcaire (*37*, 13).

Spicules.—Les spicules du tégument ventral et du tégument dorsal sont identiques. Ce sont des sortes de biscuits perforés aux extrémités (*37*, 1, 2), a bords lisses ou légèrement ondulés (*37*, 3, 4); ils peuvent devenir plus grands, percés de trois-cinq trous à l'une ou l'autre extrémité, ou aux deux extrémités (*37*, 5, 8); souvent, ils portent des digitations assez fortes, au nombre de deux à cinq (*37*, 9) et ont tendance à former des plaques (*37*, 12).

Les pieds sont renforcés par de petits bâtonnets incurvés, aux extrémités élargies et perforées (*37*, 6, 7, 10).

L'anus est armé de cinq petites dents calcaires triangulaires très épaisses et le tégument anal possède quelques plaques périproctales losangiques ou rectangulaires à petites mailles entourant cinq à six larges mailles centrales.

Les spicules des tentacules se composent uniquement de corpuscules crépus (*37*, 11, 14).

Rapports et différences.—Tant que l'échantillon, provenant de Java—et dont il n'y a pas lieu de suspecter l'origine—étudié par Semper sous le nom de *Cucumaria* sp., n'aura pas été revu, il sera impossible de savoir s'il est identique à *C. frauenfeldi* Ludwig, dont l'un des exemplaires types a été récolté au Cap de Bonne-Espérance. Par contre, *C. posthuma Lampert*, de Tafel Bay, doit entrer en synonymie avec l'espèce de Ludwig, tandis que la *Cucumaria* récoltée par Gruvel à Mossamédès, et étudiée par C. Vaney, appartient à une nouvelle espèce: *C. deichmanni* n. sp.

Cucumaria deichmanni n. sp.

Pl. *37*, figs. 16–24; pl. *38*, figs. 14–21.

Cucumaria frauenfeldi Vaney, 1911, p. 26, figs. 1–3.

Spécimen étudié.

1 ex. récolté à Swakopmund, à marée basse.

L'unique exemplaire, aux tentacules étalés, est fortement incurvé avec le bivium nettement raccourci; il a presque l'aspect des *Cucumaria frauen-*

feldi typiques. La distance dorsale de la bouche à l'anus est de 33 mm. alors qu'elle atteint 64 mm. si l'on suit le radius ventral médian; la largeur au milieu du corps est de 23 mm. et la hauteur de 20 mm. Le tégument, très plissé, est épais, non rugueux, de couleur marron très clair ventralement, bien plus foncé dorsalement. Dix tentacules, de taille égale, très ramifiés, marrons. Bouche dressée vers le haut, anus terminal dépourvu de dents calcaires.

Les pieds du bivium et du trivium sont absolument semblables, presqu'aussi nombreux sur les cinq radius, courts, cylindriques, terminés par une large ventouse non soutenue par un disque calcaire. Ils sont disposés sur quatre ou cinq rangs d'un bout à l'autre du corps. Il ne semble pas y avoir de papilles interradiales, mais l'état de contraction du corps ne permet pas de l'affirmer.

La couronne calcaire est très peu calcifiée, de forme difficile à saisir (*38*, 15): les radiales sont énormes, très déprimées au centre, non bifides au sommet et fortement encochées à la partie postérieure; les interradiales, bien plus petites, étroites, à pointe à peine encochée, sont unies aux radiales par trois à quatre pièces calcaires formant un étroit ruban. Les muscles rétracteurs simples, très puissants, s'attachent au tiers antérieur du corps. Les muscles longitudinaux sont larges, épais. Une vésicule de Poli. Un canal hydrophore situé dans le mésentère dorsal sur les deux tiers de sa longueur et terminé par un gros madréporite peu calcifié, en forme de croissant presque fermé. Gonades mâles formées d'un très grand nombre de longs tubes simples, jaune orange, envahissant toute la cavité générale.

Spicules.—Les spicules du tégument ventral et du tégument dorsal sont formés de biscuits dont les trous sont bien plus petits que ceux de *C. frauenfeldi* (*37*, 15, 16) et dont les extrémités élargies sont ondulées et ne portent jamais de digitations (*37*, 19, 22); certains biscuits sont sans perforations (*37*, 17); d'autres s'allongent (*37*, 21), possèdent parfois un assez long processus à l'une des extrémités (*38*, 17), s'élargissent (*37*, 23) pour prendre la forme de vraies plaques à deux-huit trous et plus (*38*, 18, 19, 20); ces dernières plaques sont surtout abondantes dans le tégument dorsal.

Les bâtonnets des pieds ont les extrémités élargies et plusieurs fois perforées (*37*, 18, 20, 24; *38*, 14, 16).

Les corpuscules crépus des tentacules ont tendance à prendre la forme de bâtonnets (*38*, 21).

Remarques.—Il ne semble faire aucun doute que l'exemplaire, provenant de Mossamédès, et étudié par C. Vaney, appartienne à la nouvelle espèce. Il correspond en tous points à mon exemplaire, notamment par les pieds localisés aux radius et disposés sur quatre–cinq rangées; par l'anneau calcaire à pièces radiales quadrangulaires reliées aux pièces interradiales triangulaires par une série de trois à quatre articles; par les spicules où

l'on retrouve les plaques plusieurs fois perforées de mon échantillon. Ce qu'il m'est difficile de comprendre, c'est pourquoi Vaney, qui s'était fait envoyer par le Dr. Horst, du Musée de Leyde, les types de Ludwig, a nommé son exemplaire *C. frauenfeldi*, alors qu'il s'en écarte très nettement à la fois par la forme de la couronne calcaire et par celle des spicules. Peut-être a-t-il été influencé par la presque identité de forme de son exemplaire de Mossamédès avec la forme des types de *C. frauenfeldi*?

Cucumaria insolens Théel

Pl. *39*, figs. 1–23.

Cucumaria insolens Théel, 1885, p. 70, pl. iv, fig. 5.—Vaney, 1910, p. 431.—Vaney, 1912, p. 27.—H. L. Clark, 1922, p. 411.
Cucumaria leonina var. *africana* Britten, 1910, p. 240.
Cucumaria sykion Deichmann (partim) 1948, p. 346, pl. xix, figs. 1–5.

Spécimens étudiés.

Université de Cape Town: BR. 1E, le 22–II–1940, 7 ex.; SB. 101, le 14–VII–1946, 1 ex.; SB. 102, le 14–VII–1946, 2 ex. dont 1 femelle portant des jeunes; SB. 103, le 13–VII–1946, 16 ex. dont 6 femelles portant des jeunes; SB. 104, le 14–VII–1946, 1 ex.; SB. 105, le 14–VII–1946, 1 ex.; SB. 106, le 13-VII-1946, 6 ex. dont 3 femelles portant des jeunes; LB. 121, le 15–VII–1946, 1 ex.; LB. 122, le 15–VII–1946, 3 ex.; YZ. 4D., le 5–IV–1940, 1 ex.; CH. 5F., le 8–I–1940, 4 ex.; FB. 1057 A, le 21–IV–1947, 2 ex.; FB. 1059 C, le 8–VII–1946, 4 ex. dont 1 femelle portant des jeunes; FB. 1070, le 6–VIII–1947, 4 ex.

Muséum de Paris: Cap de Bonne-Espérance, M. Delalande, 1820, 2 ex. (étiquetés *Pentacta mumia* Valenciennes, nom jamais publié); Cap de Bonne-Espérance, M. Reynaud, 1829, 5 ex. (étiquetés *P. mumia* Val.); Baie du Cap, Expédition d'Urville, MM. Quoy et Gaimard, 1828, 2 ex. (étiquetés *Cucumaria doliolum* Pallas).

Tous les échantillons sont de petite taille, le plus petit mesurant 7 mm. de long sur 4 mm. de large, le plus grand 33 mm. de long sur 5·5 mm. de large; le rapport entre la longueur et la largeur est d'ailleurs très variable suivant l'état de contraction de l'animal, et la largeur peut atteindre 13 mm. pour une longueur de 21 mm. et de 32 mm.

La coloration du tégument est généralement marron ou rouge plus ou moins foncé sur le dos, parfois presque noir, le ventre étant uniformément marron clair; cependant, certains exemplaires ont l'extrémité céphalique rouge très foncé sur la partie ventrale, le reste du trivium étant rouge clair, rosé ou même jaunâtre; trois exemplaires ont une large bande violet foncé sur le milieu du dos; un autre est uniformément rouge très foncé. Sur le vivant, d'après T. A. Stephenson (1947, p. 265), la couleur de *Cucumaria insolens* "est typiquement de couleur claire, brillante (nous l'appelions Holothurie cock-robin), variant du blanc et rose à jaune brillant, orangé et rouge". Le FB. 1057 A est indiqué comme rouge brique et brun sombre; le FB. 1070, rouge et noir; le SB. 103, gris rougeâtre.

Le tégument est toujours très rugueux, assez épais, et l'on aperçoit souvent, à la loupe, les gros nodules brillants de la couche inférieure. La forme du corps est le plus souvent subcylindrique ou en tonneau, suivant que les tentacules sont ou non invaginés. L'anus est un peu aminci, terminal ou légèrement dorsal; il n'est jamais armé de dents calcaires. Cinq exemplaires sont incurvés en C, mais ceci est certainement accidentel car il n'existe pas de raccourcissement du bivium. Les tentacules sont généralement de couleur très foncée, marrons à presque noirs, mais j'ne ai rencontrés de gris foncé et même de jaunâtres; leur nombre présente de grandes variations: il peut y en avoir dix, de taille égale; neuf grands et un plus petit situé soit dorsalement, soit ventralement, souvent réduit à l'état de moignon; un exemplaire ne possédait que neuf tentacules, deux autres seulement huit, de taille égale. La variation du nombre et de la taille des tentacules n'affecte en rien le nombre et la forme des pièces de la couronne calcaire; celle-ci (*39*, 16), petite mais bien calcifiée, se compose de dix pièces dont les médian-ventrales ne sont pas fusionnées; les radiales sont bifides antérieurement et ont leur bord inférieur fortement échancré; les interradiales, plus étroites, à pointe mousse, ont leur bord inférieur simplement ondulé.

La répartition des pieds et des papilles est très variable. Chez les plus petits exemplaires, les pieds ventraux et dorsaux sont bisériés et les interradius dorsaux possèdent de rares papilles. Chez les autres échantillons les pieds ventraux, longs, cylindriques, avec large ventouse, sont limités aux radius, bisériés, rarement sur trois-six rangs au milieu du corps; il existe assez souvent des papilles interradiales bien développées près de l'extrémité céphalique, mais il est très rare que celles-ci envahissent tout le trivium. Les pieds dorsaux, plus petits que les ventraux, sont bisériés sur les radius, mais il est parfois difficile de distinguer cette sériation tant les papilles interradiales sont nombreuses; celles-ci sont soit dispersées, soit sur huit–dix rangs longitudinaux.

L'organisation interne n'appelle aucun commentaire particulier. Il existe une vésicule de Poli, grosse et courte, souvent colorée en jaune foncé. Un seul canal hydrophore, situé dans le mésentère dorsal et terminé par un gros madréporite en forme de haricot dont les cotylédons seraient entrouverts (*39*, 19). Les gonades, en deux touffes, sont formées d'une trentaine de tubes simples, blanchâtres chez les mâles, jaune d'or chez les femelles. Les poumons, longs, fins, délicats, portent de nombreuses et courtes ramifications souvent réunies en touffes; ils débouchent dans un petit cloaque par un canal séparé. Les muscles longitudinaux sont simples, larges et plats et les muscles rétracteurs, qui s'attachent au milieu du corps, ne possèdent pas de faisceaux de fixation à la couronne calcaire.

Fait extrêmement important, onze exemplaires femelles possèdent sur

tout le dos de gros mamelons, sortes de verrues, percés d'un orifice, et dans lesquels se trouvent des jeunes plus ou moins développés; ces jeunes possèdent une couronne calcaire formée de dix pièces composées de trabécules enchevêtrées, base de la dense calcification de la couronne des adultes; il y a dix petits tentacules soutenus par des bâtonnets percés ou non à leurs extrémités (*39*, 20); les spicules du tégument se composent de grandes plaques à larges mailles (*39*, 22) et de corbeilles en voie de formation (*39*, 23). *Cucumaria insolens*, espèce incubatrice comme le sont beaucoup de *Cucumaria* antarctiques, est bien une espèce d'eau froide.

Spicules.—Les spicules du tégument sont absolument identiques à ceux figurés par Théel. Ils se répartissent en deux couches. Une couche superficielle, composée de corbeilles peut profondes, cruciformes, aux bras plus ou moins dichotomisés et portant TOUJOURS soit quatre nodules (*39*, 3), soit en plus de nombreux nodules ou épines à chaque extrémité (*39*, 4, 5, 6, 7); il est rare que ces corbeilles se ferment (*39*, 8). Une couche de boutons à quatre–huit trous, deux ou trois gros nodules centraux et huit–douze nodules périphériques (*39*, 13, 14, 15); de gros spicules très épais, portant souvent un prolongement épineux à une extrémité (*39*, 1, 2) et prenant la forme d'une pomme de pin.

Les pieds ventraux, qui possèdent un disque terminal calcaire bien développé, ont leurs parois soutenues par des bâtonnets incurvés aux extrémités percées de plusieurs petits trous et portant au centre une esquisse de troisième bras percé de un–trois trous assez grands (*39*, 21). Les pieds dorsaux et les papilles ont les mêmes bâtonnets de soutien, mais il ne semble pas y avoir de disque terminal calcaire.

Les tentacules ont de longs bâtonnets incurvés (*39*, 17, 18) et de très nombreux corpuscules crépus (*39*, 9, 10, 11, 12).

Cucumaria sinorbis n. sp.

Pl. *38*, figs. 1–13; pl. *39*, figs. 24–31.

Spécimens étudiés.

Université de Cape Town: W. 10B., 1 ex. déterminé par Miss Deichmann comme *C. insolens* Théel.
Muséum de Paris: 1 ex., Tafel Bay, M. Holub, 1880.

Les deux échantillons sont de forme subcylindrique et ont les tentacules invaginés. Le tégument épais, lisse, est uniformément marron clair. La bouche est terminale et l'anus subdorsal; celui-ci est entouré d'un cercle de petites papilles, mais ne possède ni dents anales, ni plaques périproctales. Les pieds ventraux sont disposés sur deux rangs aux extrémités, sur trois–quatre rangs au milieu du corps; ils ont une large ventouse non soutenue

par un disque calcaire. Il existe également de très nombreuses petites papilles interradiales avec une petite ventouse dépourvue aussi de disque calcaire. Les pieds dorsaux, moins nombreux que les ventraux, sont bisériés; les papilles interradiales, plus développées que les papilles ventrales et presqu'aussi grandes que les pieds dorsaux, semblent disposées sur une douzaine de lignes longitudinales.

Dix tentacules marron foncé, de taille égale. Une vésicule de Poli. Un petit canal hydrophore situé dans le mésentère dorsal et terminé par un gros madréporite sphérique, formé de pièces encastrées (*39*, 30). Les poumons atteignent les trois quarts de la longueur du corps. Les muscles longitudinaux sont larges et épais; les muscles rétracteurs, qui s'insèrent au milieu du corps, sont simples et s'attachent à la couronne calcaire par un faisceau unique. La couronne calcaire, bien calcifiée, se compose de dix pièces dont les trois médian-ventrales ne sont pas fusionnées; les radiales, à extrémité antérieure bifide, sont plus hautes que les interradiales et ont le bord postérieur fortement échancré (*38*, 8).

Spicules.—Les spicules sont de deux sortes. Dans la couche épidermique, on trouve des corbeilles nettement différentes de celles de *C. insolens*; elles se composent d'une base en forme de X à extrémités dichotomisées; la base et les extrémités n'ont jamais ni nodules, ni épines (*39*, 24, 25, 26, 28, 31); parfois, les extrémités se rejoignent pour former un cercle avec apophyses à pointes mousses (*39*, 27, 29). Il n'y a pas de boutons réguliers comme chez *C. insolens*, mais de gros sclérites dont la forme se rapproche de celle des sclérites de *C. sykion*, bien que leur taille et leur réseau secondaire les en éloigne distinctement (*38*, 1, 2, 3, 7). Les pieds sont soutenus par des bâtonnets (*38*, 13) ayant parfois un troisième bras central très réticulé (*38*, 4, 10), et des plaques très incurvées à faibles nodosités (*38*, 11). Les tentacules, qui ne possèdent jamais de corpuscules crépus, sont renforcés par des bâtonnets (*38*, 9, 12), de grandes plaques subtriangulaires (*38*, 6) et de petites plaques très incurvées (*38*, 5).

Cucumaria sykion Lampert

Pl. *40*, figs. 1–18.

Semperia sykion Lampert, 1885, p. 250.
Cucumaria sykion Théel, 1886, p. 266.—H. L. Clark, 1923, p. 412.—Deichmann, 1948, p. 346 (partim).

Spécimens étudiés.

Université de Cape Town: U 10 J., le 22–XII–1938, 1 ex.; AR. 7 C., le 23–XI–1939, 1 ex.

Les deux exemplaires, dont les tentacules sont invaginés, sont fortement contractés et prennent la forme d'un concombre incurvé. Ils sont à peu

près de même taille, le plus grand mesurant 35 mm. de long, 16 mm. dans la plus grande largeur et 14 mm. de hauteur. La bouche, festonnée, est dorsale ainsi que l'anus, et le bivium est nettement raccourci par rapport au trivium. Le tégument, épais, rugueux, est marron très foncé ou gris foncé sur le dos, marron ou gris plus clair sur le ventre.

Les pieds du trivium sont longs, cylindriques, terminés par une large ventouse de couleur brune non soutenue par un disque calcaire; ils sont très nombreux et disposés selon les radius sur cinq–six rangs; de nombreuses petites papilles occupent les interradius. Par suite de l'abondance des pieds et de l'aplatissement du trivium, l'animal semble posséder une sole ventrale et prend ainsi l'allure d'un *Psolidium*.

Les pieds du bivium, bien plus petits que ceux du trivium, sont espacés et disposés sur les radius en trois–quatre rangs; on trouve également de très nombreuses papilles dispersées dans les interradius.

L'anus est entouré d'une vingtaine de petites papilles recouvrant cinq petites dents anales, triangulaires, très épaisses. Dix grands tentacules noirs, très ramifiés, les deux ventraux légèrement plus petits. Une très grosse vésicule de Poli. Un canal hydrophore tortillonné dans le mésentère dorsal et terminé par un très gros madréporite ovoide. Gonades mâles en deux touffes de longs tubes simples, jaune foncé. Muscles longitudinaux simples, larges. Les muscles rétracteurs, qui s'attachent au tiers antérieur du corps, revêtent la forme typique signalée par Lampert: ils sont unis à la couronne calcaire par plusieurs faisceaux d'inégales épaisseurs, au nombre de quatre–sept suivant les pièces radiales considérées. La couronne calcaire se compose de dix pièces bien calcifiées (*40*, 16), les pièces médian-ventrales n'étant pas fusionnées; les radiales, non bifides au sommet, sont un peu plus longues et larges que les interradiales et ont leur bord postérieur fortement échancré alors que celui des interradiales est simplement ondulé.

Spicules.—Ce qui caractérise la *C. sykion*, c'est l'absence totale de corbeilles dans le tégument superficiel. Par ailleurs, on ne trouve jamais, dans la couche moyenne, de boutons réguliers comme chez *C. insolens*. Les gros sclérites n'ont jamais de prolongements épineux et leur architecture est totalement différente de celle des gros sclérites de *C. insolens*; les plus simples sont à plusieurs réseaux superposés percés de trois–cinq trous (*40*, 5, 6, 7, 8) ou formant comme une masse d'hémisphères superposés ou opposés (*40*, 9, 10, 14); les plus grands sont plus ou moins massifs, à faible réseau secondaire (*40*, 1, 2, 17) ou dont le réseau secondaire atteint une grande épaisseur (*40*, 3, 4); ils ne possèdent jamais les nodules centraux et périphériques comme ceux de *C. insolens*.

Les pieds, qui n'ont pas de disque terminal calcaire, sont soutenus par de nombreux bâtonnets incurvés (*40*, 12, 13). La région anale, en plus des dents calcaires, est bourrée de grandes plaques lisses (*40*, 11) à l'exclusion de

tout autre spicule. Les tentacules sont renforcés par des bâtonnets lisses (*40*, 18) ou par de grandes plaques subrectangulaires, à réseau secondaire et à grandes mailles (*40*, 15); il n'y a pas de corpuscules crépus.

Tableau comparatif des principaux caractères spécifiques de *Cucumaria insolens*, *Cucumaria sinorbis* et *Cucumaria sykion*.

Cucumaria insolens.	*Cucumaria sinorbis.*	*Cucumaria sykion.*
Jaune brillant, orangé, rouge	marron clair	marron très foncé
Pas de dents anales	Pas de dents anales	Dents anales
Pieds ventraux sur 2–6 rangs avec disque calcaire	Pieds ventraux sur 2–4 rangs sans disque calcaire	Pieds ventraux sur 5–6 rangs sans disque calcaire
Papilles interradiales ventrales	Papilles interradiales ventrales	Nombreuses papilles interradiales ventrales
Pieds dorsaux sur 2 rangs	Pieds dorsaux sur 2 rangs	Pieds dorsaux sur 3–4 rangs
Très nombreuses papilles interradiales dorsales disposées sans ordre	Très nombreuses papilles interradiales dorsales sur 10–12 rangées longitudinales	Très nombreuses papilles interradiales dorsales disposées sans ordre
Incubatrice	Non incubatrice	Non incubatrice
Faisceau unique rattachant les muscles rétracteurs à la couronne calcaire	Faisceau unique rattachant les muscles rétracteurs à la couronne calcaire	Muscles rétracteurs rattachés à la couronne calcaire par un groupe de 4–7 faisceaux
Spicules:		
Corbeilles épineuses	Corbeilles sans épines	Pas de corbeilles
Boutons réguliers	Pas de boutons réguliers	Pas de boutons réguliers
Spicules en cône de sapin avec souvent un prolongement épineux	Gros spicules jamais en forme de cône de sapin et sans prolongement épineux	Gros spicules jamais en forme de cône de sapin et sans prolongement épineux
tentacules avec corpuscules crépus	jamais de corpuscules crépus	jamais de corpuscules crépus

Cucumaria rigidapeda n. sp.

Pl. *41*, figs. 1–17.

Spécimens étudiés.

Université de Cape Town: AFR. 738 B., 1 ex. récolté le 18–VIII–1947, par 30° 22′ S.—16° 50′ E. et 101 fth. de profondeur; fond de vase vert sombre.

L'unique exemplaire est incurvé un peu comme *Cucumaria tergestina* et *Cucumaria incurvata* (*41*, 13); il mesure environ 98 mm. de long sur 9 mm. de large au niveau de la panse. Le tégument est rugueux, rigide, entièrement

rose et très brillant sous la loupe par suite de l'abondance des spicules. La bouche et l'anus sont terminaux; celui-ci est fermé par cinq dents calcaires triangulaires. Les organes locomoteurs, qui ne possèdent ni ventouse, ni disque terminal calcaire, sont donc de vraies papilles rigides, non rétractiles, coniques. Leur mode de répartition est bien spécial et est le même, qu'il s'agisse du bivium ou du trivium: ils sont très serrés, disposés sur deux rangs, sur une distance de 10 mm. à la partie antérieure; puis ils deviennent plus espacés, se disposent en quinconce sur environ 27 mm.; ensuite, sur ce que l'on pourrait appeler la panse et sur environ 32 mm., ils apparaissent bien plus longs et plus serrés; puis ils se raccourcissent et s'espacent sur la partie caudale.

Huit grands tentacules portant une trentaine de ramifications latérales, en forme de pommes de pin, sur toute la longueur du tronc. Dans la position médian-ventrale, à l'endroit où devraient se trouver deux petits tentacules, il n'y a qu'un grand espace nu. Couronne calcaire très haute, à peine calcifiée, dont les radiales sont fortement échancrées antérieurement (*41*, 9). Deux vésicules de Poli mesurant respectivement 12 mm. et 19 mm., la plus longue terminée par une grosse poche contenant une masse molle marron foncé. Un très petit canal hydrophore situé dans le mésentère dorsal. Muscles longitudinaux minces, étroits. Muscles rétracteurs très puissants, s'attachant à environ 25 mm. de la partie antérieure. Gonades situées dans la panse, formées d'une grande quantité de gros tubes longs, non ramifiés, bourrés d'ovules. Deux poumons courts, formés chacun d'un gros tronc principal marron noirâtre portant de très courtes et rares ramifications jaunâtres presque réduites à de petits nodules.

Spicules.—Les profondes corbeilles de la couche épidermique ont la base en X ou en Y; la cuvette est le plus souvent à quatre trous et le cercle périphérique a le bord externe festonné (*41*, 10, 11). Dans la couche profonde, on trouve de grandes plaques lisses à larges mailles (*41*, 1), de grandes plaques à mailles plus petites, à surface noduleuse (*41*, 2), et des plaques plus petites, subrectangulaires, triangulaires ou ovoïdes, avec un réseau secondaire plus ou moins développé (*41*, 3, 4).

Les bâtonnets des papilles ont toujours leurs extrémités percées d'un ou de deux trous; ils sont droits (*41*, 6) ou incurvés (*41*, 8) et ont parfois leur centre élargi percé d'un ou de deux trous (*41*, 5, 7).

On trouve les mêmes spicules dans la région anale que dans le tégument ventral et dorsal, mais les grandes plaques noduleuses sont bien plus nombreuses que les plaques lisses.

Les bâtonnets du tronc des tentacules sont très grands, à surface lisse, à extrémités perforées (*41*, 16, 17); ceux des ramifications sont bien plus petits et délicats (*41*, 14) et ils s'élargissent au centre (*41*, 15) allant jusqu'à prendre la forme de coupes réticulées (*41*, 12).

Rapports et différences.—Cette nouvelle espèce s'écarte franchement de tous les *Cucumariidae* jusqu'alors récoltés sur les côtes d'Afrique du Sud. Par sa forme, elle se rapproche des *Cucumaria* prenant la forme en U, et vivant généralement dans la vase, comme l'espèce européenne *Cucumaria tergestina* et certains échantillons de *Cucumaria Köllikeri*, de Dakar, et *Cucumaria rhopalodiformis* Heding, des côtes du Congo belge.

Cucumaria tetracentriophora Heding

Pl. *41*, figs. 18–22; pl. *42*, figs. 14–28.

Cucumaria tetracentriophora **Heding, 1938, p. 631, figs. 1–5.—Deichmann, 1948, p. 343, pl. xviii, figs. 4–12.**

Spécimens étudiés.

Muséum de Paris: 1 ex. Algoa Bay, M. Holub, 1880; 1 ex. Port-Elisabeth, M. Guy Babault.

Les deux exemplaires sont d'une taille à peu près égale, fortement contractés et incurvés avec raccourcissement du bivium si bien que la bouche et l'anus sont nettement dorsaux. Le plus grand exemplaire mesure 26 mm. en épaisseur; la distance de la bouche à l'anus est, par le bivium, de 40 mm., par le trivium de 90 mm. Le tégument, lisse, épais, est jaune marron avec plages marron foncé sur le bivium. La bouche est étoilée comme celle d'un *Psolidium*, mais n'est pas fermée par de vraies valves. Les tentacules, invaginés, en forme de choux-fleurs, sont au nombre de dix, de taille égale, marron foncé.

Les pieds du trivium sont disposés selon les radius sur deux rangs aux extrémités, sur quatre–cinq rangs au milieu du corps; ils sont longs, cylindriques, terminés par une large ventouse non soutenue par un disque calcaire. De petites papilles rétractées sont dispersées sur les interradius ventraux mais sont bien plus nombreuses aux approches de la bouche et de l'anus.

Les pieds dorsaux sont peu nombreux, très espacés, sur deux rangs aux extrémités, sur trois–quatre rangs au milieu du corps; il y a de très nombreuses papilles dispersées sur les interradius; les pieds et les papilles sont rétractés et n'apparaissent que comme des points brunâtres.

Une vésicule de Poli, énorme. Un canal hydrophore, situé dans le mésentère dorsal, terminé par un madréporite ovoide aux pièces encastrées (*41*, 21) presque semblable au madréporite de *Cucumaria sinorbis*. Couronne calcaire bien calcifiée (*41*, 19) et dont les pièces ventro-médianes ne sont pas fusionnées. Gonades en deux touffes de longs tubes simples jaune foncé, emplissant toute la cavité générale. Muscles rétracteurs simples, s'attachant au tiers antérieur du corps. Poumons blanc pur, très longs, très ramifiés. Petit cloaque. Anus armé de cinq grosses dents calcaires.

Spicules.—Les spicules du tégument sont de deux sortes. De très nombreux boutons, généralement à trois–quatre trous avec un nodule central et huit–dix nodules périphériques; ces boutons peuvent devenir un peu plus grands, avec dix–quinze trous, quatre–six nodules centraux et dix–vingt nodules périphériques (*42*, 14, 15, 16, 17, 18, 19); les boutons n'ont jamais la belle régularité de ceux que l'on trouve, par exemple, dans le tégument de *Cucumaria insolens.* Il y a également des bâtonnets légèrement incurvés, en forme de deux Y opposés (*42*, 20, 21, 22, 27), dont les branches peuvent être irrégulières (*42*, 23, 25, 28) et même se ramifier (*42*, 24, 26). Ces bâtonnets semblent être des corbeilles incomplètes.

Les spicules de la région anale deveinnent bien plus gros, plus massifs, presque sphériques. On trouve également de nombreuses grandes plaques périproctales très perforées, noduleuses.

Les spicules du tronc des tentacules se composent de bâtonnets très allongés, très épais (*41*, 22) pouvant devenir très larges (*41*, 18); les bâtonnets des ramifications sont plus petits, plus grêles, peu épais (*41*, 20).

Cucumaria capensis Théel

Pl. *42*, figs. 1–13.

Cucumaria capensis Théel, 1886, p. 62, pl. v, fig. 2.—Ludwig, 1887, p. 20.—Ludwig, 1887, p. 1236.—H. L. Clark, 1923, p. 412.—Ludwig et Heding, 1935, p. 171, fig. 38.—Deichmann, 1948, p. 348, pl. xix, figs. 10–12.

Spécimens étudiés.

Université de Cape Town: AFR. 775 B., 1 ex. récolté par 29° 16′ S.–14° 48′ E., et 130 fth. de profondeur; fond d'argile, de sable et de rochers.

Cet unique exemplaire, dont les tentacules sont invaginés, mesure environ 42 mm. de long sur 10 mm. dans la plus grande largeur. Le corps est vaguement pentagonal et s'effile dans la région anale. Le tégument, uniformément grisâtre, est mince, très rugueux, moucheté par suite de la présence de gros nodules calcaires. Les pieds, un peu plus nombreux ventralement que dorsalement, sont disposés en deux rangs sur chaque radius; ils sont courts, semi-rigides, terminés par une petite ventouse soutenue par un disque calcaire de dimensions réduites. Il n'y a pas de pieds dans les interradius. L'anus est entouré de cinq petites dents calcaires à peine visibles.

Les tentacules, au nombre de dix dont deux ventraux un peu plus petits, sont grands, très ramifiés. La couronne calcaire, très peu calcifiée, semble identique à celle figurée par Théel. Un canal hydrophore libre, terminé par un très gros madréporite. Une vésicule de Poli, sphérique. Les gonades sont formées d'un grand nombre de longs tubes assez gros, non ramifiés. Les poumons atteignent la moitié de la longueur du corps; ils se

composent d'un tube rubané tacheté de brun, portant tous les trois à cinq millimètres, et d'un seul côté du tube, des digitations à deux courtes branches. Les muscles longitudinaux sont larges et minces; les muscles rétracteurs s'attachent à la moitié du corps.

Spicules.—Les spicules du tégument ventral et du tégument dorsal sont identiques et répartis en deux couches. La couche externe est composée de délicates corbeilles percées de un–quatre trous (*42*, 5, 6, 7, 8, 9). La couche interne comprend des boutons à quatre trous et à deux–trois gros nodules centraux (*42*, 3) ou à six–dix trous et de nombreux nodules centraux et périphériques (*42*, 4); ces derniers boutons peuvent atteindre une assez grande taille et on trouve tous les termes de passage entre les boutons de la figure 4 et les énormes spicules de la fig. 1, de forme losangique ou subrectangulaire, massifs et très noduleux.

La région anale possède les mêmes spicules que le tégument avec, en plus, de grandes plaques allongées, avec quelques nodules à une extrémité ou sans nodules ni réseau secondaire, percées de trente–soixante trous disposés sur deux–quatre rangées longitudinales. Il existe également des plaques à bords très échancrés, dont la forme se rapproche de celle des corbeilles, mais qui sont bien plus grandes (*42*, 2). Les dents anales, très petites, sont épaisses et finement réticulées.

Les parois pédieuses sont renforcées par des bâtonnets, droits ou incurvés, avec (*42*, 12) ou sans nodules (*42*, 13). On trouve aussi, et en assez grand nombre, des plaques au centre élargi, avec ou sans nodules. La ventouse terminale est soutenue par un petit disque calcaire.

Dans les tentacules, il y a de nombreux bâtonnets droits ou incurvés, sans nodules (*42*, 10), et de petites plaques concaves, avec ou sans nodules (*42*, 11).

Remarques.—*Cucumaria capensis* n'avait été trouvée jusqu'ici que dans les eaux voisines du Cap de Bonne-Espérance, par 98–230 fth. de profondeur. Sluiter a appelé *Cucumaria capensis* six exemplaires d'une Holothurie récoltée dans la mer des Célèbes, la mer de Banda et dans le détroit de Molo. Des différences dans les spicules me font croire qu'il ne s'agit pas de *Cucumaria capensis* mais d'une forme voisine de *Cucumaria capensis* var. *parva* Mitsukuri et de *Cucumaria tegulata* Augustin, toutes deux des côtes japonaises.

Genre PENTACTA Goldfuss, 1820.

Pentacta Goldfuss, 1820, p. 177.
NON:
- **Colochirus Troschel, 1846, p. 64.**
- **Cercodemas Selenka, 1867, p. 243.**

Corps subcylindrique à tégument épais bourré de spicules, peu contractile. Bouche terminale simplement étoilée. Dix tentacules de taille

égale. Anus terminal armé de cinq dents calcaires triangulaires. Pieds ventraux disposés sur deux rangs serrés le long des radius. Pieds dorsaux plus petits, moins nombreux, bisériés. Pas de papilles interradiales. Pas de sole ventrale. Couronne calcaire très forte, sans prolongements postérieurs et dont les trois pièces ventro-médianes ne sont pas fusionnées. Une vésicule de Poli. Un canal hydrophore. Spicules du tégument comprenant une couche externe de délicates plaques réticulées portant de fines excroissances sur toute la surface; jamais de vraies corbeilles. Couche interne de boutons et de gros spicules.

Pentacta doliolum (Pallas)

Pl. *43*, figs. 1–15.

Actinia doliolum Pallas, 1766, p. 152, pl. ii, figs. 10–12.
Pentacta doliolum Goldfuss, 1820, p. 177.—H. L. Clark, 1923, p. 416.—Deichmann, 1930, p. 180.—Deichmann, 1948, p, 352, pl. xx, figs. 1–6.
Colochirus doliolum Marenzeller, 1874, p. 303.—Ludwig, 1887, p. 13.
Cucumaria discolor Théel, 1886, p. 64, pl. iv, fig. 8.—Britten, 1910, p. 239.—H. L. Clark, 1923, p. 410.—Deichmann, 1930, p. 180.

Spécimens étudiés.

Université de Cape Town: SB. 99, le 13–VII–1946, 5 ex.; SB. 100, le 13–VII–1946, 2 ex.; LB. 123, le 16–VII–1946, 1 ex.; TB. 81 A, le 4–VII–1946, 22 ex.; TB. 84 B, le 11–II–1947, 3 ex.; TB. 85 A, le 25–X–1946, 2 ex.; TB. 86 A, le 25–X–1946, 1 ex.; TB. 88 B, le 25–X–1946, 12 ex.; TB. 92 D, le 3–VII–1947, 7 ex.; TB. 98, le 25–XI–1948, 3 ex.; FB. 1057 B, le 21–IV–1947, 1 ex.
Muséum de Paris: Cap de Bonne-Espérance, MM. Quoy et Gaimard, 1829, 4 ex.

Des soixante-trois exemplaires que j'ai étudiés, le plus petit mesurait 11 mm. de long sur 4 mm. de large, le plus grand 95 mm. de long sur 23 mm. de large. La plupart ont leurs tentacules étalés. Le corps est subcylindrique. Le tégument est lisse, de couleur uniformément violet sombre à brun noir sur le dos, violet plus clair avec larges plages jaunâtres sur le ventre. Le péristome est haut et dépourvu de tout organe locomoteur.

Les pieds du trivium sont longs, larges, terminés par une large ventouse soutenue non pas par un unique disque calcaire, mais par une dizaine de petites plaques disposées en cercle, plus ou moins imbriquées, entourant un disque calcaire très réduit chez les pieds dorsaux, un peu plus grand chez les pieds ventraux; ces pieds sont disposés en deux rangs serrés sur les radius. Il n'y a pas de papilles interradiales.

Les pieds du bivium sont petits, coniques, disposés également sur deux rangs selon les radius, mais moins nombreux que les pieds ventraux.

La bouche et l'anus sont terminaux; celui-ci est fermé par cinq dents triangulaires à pointe mousse. Les tentacules, au nombre de dix, sont

grands, très ramifiés, de taille égale, noirâtres ou marron foncé. La couronne calcaire (*43*, 13) est formée de dix pièces dont les trois ventro-médianes ne sont pas fusionnées; les radiales sont hautes, étroites, à sommet antérieur bifide, à bord postérieur échancré; les interradiales sont minces, triangulaires, à bord postérieur fortement ondulé.

Une grosse vésicule de Poli. Un canal hydrophore tortillonné dans le mésentère dorsal, terminé par un gros madréporite sphérique. Muscles longitudinaux simples, larges, peu épais. Muscles rétracteurs simples, s'attachant au milieu du corps. Gonades en deux touffes de longs tubes jaunâtres, non ramifiés. Poumons très grands, très ramifiés, débouchant dans un petit cloaque par deux canaux distincts. Les vésicules pédieuses sont petites, translucides.

Spicules.—Le tégument est bourré de spicules. Ce sont des boutons dont les plus simples sont subcarrés, percés de quatre trous avec un nodule central et huit nodules périphériques (*43*, 3) ou plus allongés, avec quatre trous, trois à cinq nodules centraux et dix-douze nodules périphériques (*43*, 4); ces boutons peuvent devenir plus grands, à nodules plus petits mais à plus larges mailles (*43*, 2) ou s'épaissir par superposition de plusieurs réseaux réticulés (*43*, 1). On trouve également de très petits boutons ressemblant à des corbeilles (*43*, 5, 7, 8, 9) qui, vus de profil, sont couverts de fines excroissances (*43*, 6).

Le tégument dorsal, en plus des spicules énumérés ci-dessus, possède d'énormes spicules extrêmement massifs, presqu'aussi épais que longs, formés d'un grand nombre de réseaux noduleux superposés; ils ressemblent vaguement à une mûre.

Le tégument anal comprend toutes ces sortes de spicules et, aussi, de grandes plaques périproctales lisses, avec une simple esquisse de réseau secondaire ou portant au centre de faibles nodosités qui peuvent prendre un grand développement, couvrir toute la surface de la plaque et se compliquer d'un ou plusieurs réseaux secondaires.

Les bâtonnets de soutien des pieds ventraux sont très réticulés, à centre fortement élargi, à surface unie (*43*, 10) mais aussi très souvent noduleuse (*43*, 12).

Les bâtonnets des tentacules sont très longs (*43*, 11) et, dans les digitations, on trouve des plaques treillissées très incurvées (*43*, 14) ou droites at à surface portant quelques faibles nodules périphériques (*43*, 15).

Genre Thyone Oken, 1815.

Corps petit ou de taille moyenne, à peau molle, couvert de pieds répartis aussi bien sur les radius que sur les interradius, souvent un peu plus nombreux ventralement que dorsalement. Bouche terminale entourée de dix

tentacules dont les ventro-médians sont plus petits. Anus terminal armé de cinq dents calcaires triangulaires. Couronne calcaire très haute, formée de petites pièces, à prolongements caudaux généralement très longs. Une à quatre vésicules de Poli. Un canal hydrophore. Spicules: Tourelles à flèche formée de deux à quatre piliers ou courts bâtonnets perforés aux extrémités, ou les deux à la fois. Souvent, les spicules sont résorbés dans les grands exemplaires et ne subsistent plus que dans la région anale.

Thyone proceracorona n. sp.

Pl. *44*, figs. 1-16.

Spécimens étudiés.

Université de Cape Town: TB. 81 A2, le 4-VIII-1946, 1 partie céphalique.

Je n'ai malheureusement en ma possession qu'un fragment de corps comprenant les tentacules, le péristome et la couronne calcaire, et environ 1 cm. de tégument proprement dit, ce qui ne me permet pas de donner d'indications sur la forme du corps et l'organisation interne. Mais les spicules sont si typiques que, malgré ces lacunes, je n'ai pas hésité à nommer cette nouvelle espèce qui sera à rechercher au même endroit. Cet unique fragment était mélangé à un lot de *Pentacta doliolum*.

Les pieds sont répartis sur l'ensemble du tégument, sans sériation apparente; ils sont assez nombreux, longs, cylindriques, terminés par une ventouse soutenue par un grand disque calcaire. Le tégument est grisâtre. Il y a huit grands tentacules très ramifiés et deux très petits tentacules centraux, de couleur marron clair.

La couronne calcaire (*44*, 5) est très haute; les radiales sont bifides au sommet alors que les interradiales sont triangulaires à pointe vive. Les pièces ventro-médianes sont fusionnées. Les pièces radiales possèdent de très longs prolongements postérieurs, formés de pièces calcaires disposées en échelle alors que les particules de la couronne elle-même sont disposées en mosaïque.

Spicules.—Le tégument de la partie orale possède de petits spicules bizarremment contournés, percés d'un seul trou à l'une des extrémités (*44*, 9, 10, 11). Les parois des pieds et le tégument renferment des bâtonnets toujours incurvés, à surface tourmentée (*44*, 1); l'une des extrémités (*44*, 3) ou les deux extrémités (*44*, 2) peuvent être coudées à angle droit. D'autres possèdent un prolongement dichotomisé, partant du milieu du corps du spicule et parallèle à la branche distale (*44*, 4). Les tourelles sont massives, d'abord très simples à bras dans le même prolongement (*44*, 7) ou contournés, bifides, faisant un angle avec l'horizontale (*44*, 8); ces tourelles deviennent plus hautes, plus compliquées, à surface portant de grosses excroissances coniques, à flèche à trois-quatre piliers terminés par cinq-dix pointes (*44*, 14,

15, 16). Le disque calcaire des pieds est à bord dentelé, à trous centraux très petits suivis immédiatement de trous bien plus grands qui se rétrécissent à la périphérie (*44*, 6).

Les tentacules sont renforcés par des bâtonnets (*44*, 13) qui souvent s'élargissent et possèdent une esquisse de troisième bras médian (*44*, 12).

Rapports et différences.—Thyone proceracorona ressemble à *Thyone aurea* par sa couronne calcaire très développée et la forme du disque calcaire des pieds. Mais elle s'en éloigne, aussi bien que de *Thyone articulata*, par ses spicules de forme si spéciale.

Thyone aurea (Quoy et Gaimard)

Pl. *45*, figs. 1-28; pl. *46*, figs. 1-2, 6-7.

Holothuria aurea Quoy et Gaimard, 1833, p. 120, pl. vii, figs. 15-17.
Thyone aurea Semper, 1867, p. 66.—Lampert, 1885, p. 163.—Théel, 1886, p. 141.—
Deichmann, 1948 (partim), p. 354, text-figs. 1-5, pl. xix, figs. 13-18.
Cladolabes aureus Brandt, 1835, p. 74.
Thyone serratus Britten, 1910, p. 242.
Thyone serrata H. L. Clark, 1923, p. 415.

Spécimens étudiés.

Université de Cape Town: TB. 81 B, le 4-VIII-1946, 4 ex.; TB. 83 B, le 11-II-1947, 6 ex.; TB. 85 B, le 25-X-1947, 1 ex.; TB. 93 B, le 3-VII-1947, 1 ex.; SB. 95, le 13-VII-1946, 3 ex.; SB. 96, le 14-VII-1946, 1 ex.; SB. 97, le 14-VII-1946, 1 ex.; SB. 98, le 14-VII-1946, 1 ex.; LB. 119, le 15-VII-1946, 1 ex.; LB. 120, le 27-IV-1948, 2 ex.; sept exemplaires récoltés à Springfontein, entre Blaauberg et Yserfontein, le 25-I-1948 (rejetés par la tempête).

Les échantillons que j'ai examinés ont leurs tentacules soit étalés, soit invaginés. Le plus petit exemplaire mesure 18 mm. de long sur 5 mm. de large, le plus grand 115 mm. de long sur 20 mm. de large. Sept exemplaires sont réduits aux tentacules, à la couronne calcaire et à un ou deux centimètres de tégument. Le corps est subcylindrique à anus légèrement effilé. Le tégument est épais, lisse, grisâtre à violacé ou uniformément orange, ou blanc jaunâtre avec plages violacées, ou rougeâtre. Les tentacules, au nombre de dix, sont marron foncé; il y en a huit très grands et deux très petits situés dans le radius ventral médian. La membrane péristomienne, dépourvue de pieds, atteint 1 cm. de hauteur et plus. Les pieds dorsaux et ventraux sont identiques, nombreux mais cependant assez espacés, répartis sur tout le corps; ils sont courts, terminés par une large ventouse soutenue par un disque calcaire à bord échancré, percé au centre de petits trous suivis immédiatement de trous bien plus larges (*46*, 1). Cinq sillons brunâtres très étroits délimitent les radius, sans qu'il y ait plus grande abondance ou sériation des pieds dans ces régions.

La couronne calcaire (*45*, 23) se compose de dix pièces très hautes, dont

les ventro-médianes sont fusionnées. Les pièces interradiales sont triangulaires, à pointe vive; les radiales ont l'extrémité antérieure subtriangulaire et bifide, et portent deux longs prolongements postérieurs; l'ensemble de la couronne est formé de très nombreuses petites pièces disposées en mosaïque. Suivant les exemplaires, il y a le plus souvent une seule vésicule de Poli, parfois deux très grosses; un échantillon avait quatre vésicules dont deux grosses et deux bien plus petites. Tous les exemplaires ont un seul canal hydrophore très petit, situé dans le mésentère dorsal et terminé par un gros madréporite sphérique. Muscles longitudinaux larges. Muscles rétracteurs simples, s'attachant au tiers antérieur du corps. Petite papille génitale débouchant entre deux tentacules dorsaux. Gonades mâles formées d'un très grand nombre de tubes orangés. Pharynx et estomac très musculeux. Poumons énormes, atteignant la longueur du corps, très ramifiés. Très grand cloaque. Anus armé de cinq petites dents triangulaires très épaisses.

Spicules.—Les spicules du tégument sont assez rares. Ce sont des bâtonnets en voie de formation (*45*, 1, 9, 10), dont l'extrémité s'élargie et est percée d'un trou assez grand, les bords des extrémités portant deux à six courtes digitations (*45*, 2, 3); ces digitations prennent souvent un grand développement (*45*, 17) alors que la tige du bâtonnet se raccourcit (*45*, 19). Dans le tégument dorsal, surtout, les bâtonnets portent, en leur partie centrale, une épine ou nodule (*45*, 4, 7, 8, 11); une des extrémités peut également se dichotomiser en deux ou plusieurs longs processus (*45*, 12, 13). On trouve aussi des plaques percées de trous inégaux, à surface lisse (*45*, 5, 14, 18), noduleuse (*45*, 6, 15, 20) ou avec un réseau secondaire donnant à ces corpuscules l'aspect de coupes irrégulières (*45*, 21); quelques-unes de ces plaques peuvent devenir assez grandes (*45*, 27).

La région anale possède de grandes plaques périproctales très réticulées, ovoïdes, subrectangulaires ou subtriangulaires avec, parfois, un réseau secondaire bien développé. Par ailleurs, on y trouve des plaques losangiques, à bords portant de courtes digitations, à surface avec deux–trois épines (*45*, 16), ayant, de plus, soit une esquisse de réseau secondaire (*45*, 22) soit une flèche centrale terminée par un bouquet de pointes (*45*, 24, 26); cette flèche est assez haute, massive, percée de un ou plusieurs trous (*45*, 25, 28). D'autre part, le disque terminal des pieds anaux devient très grand.

Les bâtonnets des tentacules, peu nombreux, sont petits (*46*, 2, 7); on trouve aussi des plaques allongées, lisses (*46*, 6) ou portant des nodules périphériques; à la base des tentacules sont disposées de petites plaques ovales à quatre trous centraux et six–huit trous aux extrémités.

Remarques.—La plupart des types de Quoy et Gaimard sont encore conservés au Muséum de Paris et leur redescription est actuellement en

cours de publication. Malheureusement, celui de *Holothuria aurea* a disparu et doit être considéré comme définitivement perdu. A quelle *Thyone* correspondait-il ? Il semble raisonnable de se ranger à l'avis de la plupart des auteurs et, notamment, de considérer que la *Thyone* décrite par Miss Deichmann (1948, p. 354) est bien *Thyone aurea* (Quoy et Gaimard). Afin d'éviter toute confusion, je propose de considérer comme Neotype l'échantillon LB. 120 nº 1, qui sera rangé au Muséum de Paris dans la collection des types de Quoy et Gaimard.

Thyone articulata Vaney

Pl. *46*, figs. 3–5, 8–19.

Thyone articulata Vaney, 1908, p. 295.—Vaney, 1908, p. 426, pl. iv, figs. 43–44.
Thyone aurea Deichmann, 1948 (partim), p. 354, text-figs. 6–9.

Spécimens étudiés.

Université de Cape Town: TB. 81 B, le 4–VIII–1946, 4 ex.; TB. 97, le 11–II–1947, 1 ex.

Les cinq exemplaires, dont quatre se trouvaient mélangés à des *Thyone aurea*, mesurent, le plus petit 10 mm., le plus grand 47 mm. de long. Le tégument est assez épais, lisse, de couleur marron violet plus ou moins foncé, sauf celui du petit exemplaire qui est blanc jaunâtre. La bouche est terminale et l'anus légèrement effilé. Les tentacules sont au nombre de dix dont deux ventro-médians beaucoup plus petits. Les pieds sont courts, cylindriques, terminés par une ventouse soutenue par un disque calcaire tout-à-fait typique et sur lequel nous reviendrons tout à l'heure; ces pieds sont nombreux et répartis sans ordre sur tout le corps. La couronne calcaire (*46*, 16) est petite, bien calcifiée, avec les pièces ventrales coalescentes; les radiales sont à pointe bifide et portent deux longs prolongements caudaux; les interradiales sont triangulaires; le corps même de la couronne est formé par l'assemblage de quelques pièces calcaires. Une vésicule de Poli. Un canal hydrophore. Muscles longitudinaux larges, épais. Muscles rétracteurs s'attachant au cinquième antérieur du corps. Gonades formées de deux touffes de quelques tubes fins, non ramifiés, jaune pâle. Poumons atteignant presque la longueur du corps, très ramifiés. Vaste cloaque. Anus armé de cinq petites dents calcaires.

Spicules.—Ce qui caractérise du premier coup d'oeil *Thyone articulata*, c'est la grandeur et la forme du disque terminal calcaire des pédicelles; celui-ci (*46*, 3) est bien plus petit que ceux des pieds de *Th. proceracorona* et de *Th. aurea*, puisque son diamètre ne dépasse pas 11°μ alors qu'il atteint 220 μ chez les deux autres espèces; De plus, son bord est parfaitement lisse; enfin, détail essentiel, on trouve au centre de nombreux petits trous et de grandes ouvertures rayonnantes à la périphérie.

Les spicules du tégument, peu nombreux, se composent de bâtonnets plus petits, plus délicats que ceux de *Thyone aurea* (*46*, 8, 9, 10, 12); leurs digitations, lorsqu'elles existent, sont courtes (*46*, 11); leurs extrémités peuvent s'élargir et être percées chacune de deux–cinq petits trous (*46*, 4, 5, 13). On trouve, dans la région anale, des plaques lisses (*46*, 18) ou portant un nodule (*46*, 14) et, aussi, quelques grandes plaques périproctales. Il n'y a jamais de colonnettes ni de tourelles dans le tégument.

Les tentacules sont renforcés par de grandes plaques ou des bâtonnets (*46*, 15, 17, 19).

Remarques.—Les types de *Thyone articulata* ont été récoltés dans la Baie de Saldanha, par 9–10 brasses de profondeur. L'un des deux exemplaires, le plus petit, est conservé au Musée Océanographique de Monaco et j'ai pu l'examiner grâce à l'obligeance de M. Belloc, qui a bien voulu me le faire parvenir. Malheureusement, il n'y a plus de spicules dans le tégument et la couronne calcaire elle-même a presqu'entièrement été dissoute. Il se peut que l'autre type soit mieux conservé, mais je n'ai pu savoir où il se trouvait. Aussi, ai-je dû, pour identifier mes *Thyone*, me contenter de la description et des figures de Vaney. Les bâtonnets du tégument sont identiques. Les anneaux calcaires se ressemblent, bien que Vaney figure des radiales non incisées au sommet. Enfin, cette phrase de Vaney: "les pédicelles ont une plaque terminale avec de nombreuses petites perforations centrales et de grandes ouvertures rayonnantes placées à la périphérie", lève tous les doutes qui auraient pu subsister quant à l'identité de mes échantillons et des types de *Th. articulata.*

Th. aurea et *Th. articulata* ont dû souvent être confondues et il est bien difficile de se prononcer pour établir une synonymie lorsque les auteurs ne donnent ni figures, ni description détaillée. Il faudra donc revoir tous les exemplaires déterminés comme *Th. aurea* pour faire une discrimination parmi les échantillons ayant donné lieu à publication.

Genre OPHEODESOMA Fisher, 1907.

Quatorze à seize tentacules pinnés, portant de dix à soixante-dix digitations de chaque côté, unies ou non par une membrane. Nombreux tubes hydrophores répartis autour du canal oral. Nombreuses vésicules de Poli. Couronne cartilagineuse souvent présente. Pièces radiales de la couronne calcaire percées pour le passage des nerfs. Spicules: présence ou non de baguettes dans les tentacules et le disque oral; plaques d'ancres larges, percées d'un large trou central et de six trous marginaux, tous plus ou moins dentelés; l'extrémité de la plaque s'amincit brusquement; les ancres sont grandes: les bras de l'arc n'ont pas de denticulations alors que

le sommet porte de nombreux granules; la manivelle de l'ancre se divise en six-huit courtes ramifications épineuses.

Opheodesoma mauritiae Heding, 1928

Pl. *47*, figs. 1–18.

***Opheodesoma mauritiae* Heding, 1928, p. 130, figs. 4 (1), 6 (14–17) et 7 (4, 10).**
***Opheodesoma africana* Heding, 1931, p. 645, figs. 2 (2, 6–11).**
***Synapta serpentina* Lampert, 1896, p. 64.**

Spécimens étudiés.

Université de Cape Town: Inhaca, Delagoa Bay (Est Afrique portuguais), 2 ex.

Les deux exemplaires mesurent respectivement 600 mm. et 900 mm. de longueur. Le tégument est mince, rugueux, gris avec bandes transversales plus ou moins régulières, marrons et gris foncé sur le dos, gris très clair avec plages blanchâtres sur le ventre. Le plus petit échantillon a quinze tentacules, l'autre dix-sept; ceux-ci sont très grands et portent de cinquante à soixante-dix paires de digitations non unies par une membrane. La couronne calcaire (*47*, 12) est blanc pur, non inclue dans une couronne cartilagineuse proprement dite mais enfermée dans une enveloppe translucide; elle est composée de quinze pièces: les radiales sont triangulaires, percées d'un large trou irrégulier; les interradiales sont en massue, bien plus petites et plus étroites que les radiales; le bord postérieur de la couronne est fortement ondulé. Très nombreuses vésicules de Poli de moyenne longueur et un grand nombre de petits canaux hydrophores. Les muscles longitudinaux, très puissants, s'élargissent en une foliole amincie aux approches de la couronne calcaire. L'intestin forme une boucle vers le milieu du corps. Gonades formées de très longs tubes fins, deux à trois fois ramifiés. Les urnes ciliées, extrêmement nombreuses, sont situées sur les mésentères; elles sont toutes de la même forme et de même taille (*47*, 3, 6, 7), isolées ou réunies en amas de dix à vingt.

Spicules.—Le tégument est bourré de granules miliaires (*47*, 8, 10). Les plaques d'ancres de la région orale sont presqu'aussi hautes que larges, percées de sept grands trous aux bords fortement dentelés (*47*, 2); la partie basilaire, percée de deux trous (*47*, 2, 5) est surmontée d'un pont très simple, généralement non perforé. Les plaques d'ancres de la région moyenne et postérieure sont plus grandes et bien moins trapues; la partie basilaire, large, est percée de cinq–six petits trous (*47*, 1), soit de quelques grands trous accompagnés de petites perforations (*47*, 4, 9); le pont, très simple, a les bords légèrement festonnés. Les ancres sont identiques pour les deux formes de plaques (*47*, 11); leurs bras sont dépourvus de denticulations mais le sommet

porte de huit à dix petites dents rectangulaires; la partie basilaire est huit-dix fois ramifiée, chaque apophyse étant fortement dentelée et portant, en plus, de petites épines (*47*, 13, 14).

Les tentacules ont uniquement des granules miliaires, identiques à ceux du tégument; par contre, le disque oral est renforcé par de courts bâtonnets non perforés, à pointe mousse (*47*, 15, 17) ou portant de fines dentelures (*47*, 16, 18).

Rapports et différences.—Le genre *opheodesoma* comporte dix espèces, dont deux ont été récoltées dans les eaux africaines: *O. mauritiae* Heding, 1928, de l'Ile Maurice, et *O. africana* Heding, 1931, de Zanzibar, qui me semble identique à la première et que je mets en synonymie de celle-ci. Il est curieux de constater que lors de sa description d'*O. africana* Heding ne pense pas à comparer ses échantillons de Zanzibar avec les types de *O. mauritiae* de l'Ile Maurice, tandis qu'il les rapproche de *O. serpentina*, des Célèbes, et de *O. lineata*, du Golfe de Siam.

Les exemplaires récoltés à Delagoa Bay ressemblent en tous points aux échantillons types de *O. mauritiae* et à ceux de *O. africana*.

Genre Epitomapta Heding, 1928.

Habituellement, douze tentacules pinnés. Organes sensoriels jamais sous forme de tache oculaire, mais comme des coupes sensorielles situées sur le côté oral des tentacules. Couronne calcaire bien développée; les pièces radiales ne sont pas perforées pour le passage des nerfs, mais ont seulement une encoche sur le bord antérieur. Pas de couronne cartilagineuse. Une seule vésicule de Poli. Un canal hydrophore non ramifié. Urnes ciliées de formes différentes, disposées seulement sur la paroi du corps et non pas sur les mésentères. Spicules: dans le tégument, ancres, plaques d'ancres, granules miliaires; bâtonnets dans les tentacules.

Epitomapta knysnaensis n. sp.

Pl. *48*, figs. 8–14.

Spécimens étudiés.

Université de Cape Town: KNY. 33 B, le 17–VII–1947, 1 ex.; KNY. 36 G, le 18–VII–1947, 2 ex.

Les trois exemplaires mesurent respectivement 28 mm., 37 mm. et 40 mm. de longueur. Le tégument est mince, lisse, gris rosé. Les tentacules, au nombre de douze, de taille égale, sont petits et portent cinq paires de digitations et une digitation terminale bien plus longue; on dénombre de zéro à douze organes sensoriels sur le tronc des tentacules. La couronne calcaire (*48*, 9) est formée de douze pièces; radiales triangulaires

mais non perforées pour le passage des nerfs, bien que la radiale ventro-médiane porte un profond évidement non perforé. L'intestin est droit. Il existe soit une, soit deux vésicules de Poli et un assez long canal hydrophore. Les gonades sont formées de deux ou trois tubes très gros, courts, à extrémité parfois biramifiée. Les urnes ciliées se trouvent disposées sur une seule ligne sur le tégument de l'interradius dorsal médian; elles sont de deux tailles, jamais en touffes (*48*, 12).

Spicules.—Les ancres et les plaques d'ancres sont, pour la plupart, fortement attaquées. Les plaques d'ancres sont de deux sortes; les unes, grandes, ovales, sont percées de sept trous centraux à bords légèrement denticulés, de deux grands trous et de six-huit trous bien plus petits à la base; il n'y a pas de pont (*48*, 8); les autres plaques, plus trapues, ont également sept trous centraux mais les denticulations sont bien mieux marquées, subcarrées; la base de la plaque est percée de deux larges trous séparés par un petit trou ovoide sous lequel sont disposées trois petites perforations; il n'y a pas de vrai pont (*48*, 10). L'ancre a les bras armés de cinq denticulations; le sommet est lisse, la base fortement ondulée mais sans aspérités à pointes vives (*48*, 8). Il y a de très nombreux bâtonnets dans les bandes radiales (*48*, 11). Les bâtonnets des tentacules sont incurvés, à extrémités dichotomisées mais jamais perforées (*48*, 13, 14).

Rapports et différences.—Le genre *Epitomapta*, créé par Heding en 1928, ne comportait jusqu'ici que deux espèces: *E. roseola* (Verrill), du Massachusetts et des Bermudes, et *E. tabagoe* Heding, de la côte pacifique du Panama. C'est après bien des hésitations que j'ai rapporté l'espèce d'Afrique du Sud au genre *Epitomapta*, car si la couronne calcaire n'est pas perforée, ce sont des bâtonnets que l'on trouve dans les bandes radiales et non des granules ovoides perforés; de plus, les baguettes des tentacules ne sont pas perforées aux extrémités et il peut y avoir deux vésicules de Poli. Peut-être *E. knysnaensis* appartient-elle à un nouveau genre, mais le matériel en ma possession n'est pas suffisant pour l'affirmer.

Par ailleurs, l'espèce décrite par Miss Deichmann, en 1948, sous le nom de *Leptosynapta* sp., et provenant de Buffel's River, appartient peut-être au même groupe que *E. knysnaensis*, mais l'absence de toute description de l'organisation interne ne permet pas de l'affirmer.

Genre Taeniogyrus Semper, 1868

Dix à douze tentacules peltés-digités, portant cinq à sept digitations de chaque côté, avec une paire terminale plus longue. Sexes séparés; une seule espèce hermaphrodite; gonades formées de tubes simples ou ramifiés. Pièces radiales de la couronne calcaire non perforées pour le passage des nerfs. Une ou plusieurs vésicules de Poli. Aucun organe gustatif. Urnes

ciliées sur les mésentères ou sur la paroi du corps. Spicules consistant en roues réunies dans des papilles et en corps sigmoides groupés ou non. Pas de granules miliaires dans la peau ou dans les muscles longitudinaux.

Taeniogyrus dayi n. sp.

Pl. *48*, figs. 1–7.

Spécimens étudiés.

Université de Cape Town: FB. 1051 B, le 30–I–1947, 8 ex. brun rouge avec tentacules pâles; FB. 1066, le 19–IV–1948, 2 ex. pourpres; LB. 154, le 15–VII–1946, 3 ex.

Tous les exemplaires sont plus ou moins fragmentés; le plus grand fragment, portant les tentacules, mesure 50 mm. de long et 4 mm. de large à la partie céphalique. Le tégument est mince, violacé, portant des verrucosités violet sombre, très serrées; ces verrucosités peuvent s'estomper jusqu'à disparaitre presque complètement sur certains fragments. L'animal vivant est indiqué comme étant pourpre à brun rouge, les tentacules étant bien plus clairs; ceux-ci, au nombre de dix de taille égale, portent chacun trois ou quatre paires de digitations latérales de taille croissante en partant de la base des tentacules, la dernière paire étant la plus grande. On trouve à la base de chaque tentacule un organe sensoriel en forme de verrue violet sombre.

La couronne calcaire est formée de dix pièces (*48*, 5); les radiales, non perforées, sont subrectangulaires à sommet encoché; les interradiales sont triangulaires. L'intestin forme une boucle. Muscles longitudinaux larges. Une grosse vésicule de Poli. Un très petit canal hydrophore. Les gonades se composent d'une dizaine de gros tubes très longs, simples, à peu près semblables qu'il s'agisse des tubes mâles ou des tubes femelles, et bourrés d'oeufs ou de spermatozoides; les sexes sont séparés. Les urnes ciliées (*48*, 7) sont très nombreuses sur le mésentère dorsal, mais ne semblent pas réunies en touffes; elles ont toutes même forme et même taille.

Spicules.—Les spicules du tégument comprennent des roues et des corps sigmoides. Les roues, à peu près toutes de la même taille, sont dispersées ou en amas d'une vingtaine de roues réunies dans les verrucosités. Elles sont ou non percées d'un trou central (*48*, 1) mais qui ne traverse pas (*48*, 2). Les corps sigmoides, nombreux, ne sont jamais en amas; ils sont dispersés et on les rencontre même dans les bandes radiales (*48*, 3, 4). Les tentacules sont renforcés par des bâtonnets incurvés, aux extrémités dentelées et jamais perforées (*48*, 6).

Rapports et différences.—Le genre *Taeniogyrus* ne comportait jusqu'ici que six espèces. Deux d'entre elles, *T. contortus* (Ludwig) et *T. dubius*

Clark, possèdent douze tentacules. Les autres, *T. australianus* (Stimpson), *T. cidaridis* Ohshima, *T. keiensis* Heding et *T. clavus* Heding n'en ont que dix. Aucune de ces espèces n'appartient à l'Atlantique sud; *T. contortus* a été trouvé dans une zone allant des Kerguelen au Cap Horn; les autres proviennent d'Australie, d'Océanie et des Iles Hawaii. Sauf *T. contortus* et *T. australianus*, récoltés par 3–20 mètres, les autres espèces ont été ramenées de fond allant de 80 mètres à 400 mètres et plus.

Taeniogyrus dayi se rapproche, par la forme des spicules, de l'espèce antarctique *T. contortus*, mais on n'y trouve jamais de corps sigmoides anormaux; de plus *T. contortus* possède douze tentacules, sept vésicules de Poli et est hermaphrodite. La couronne calcaire de *T. keiensis*, des Moluques, ressemble beaucoup à celle de *T. dayi*, mais c'est le seul point commun aux deux espèces; enfin, *T. australianus* comme *T. dayi* n'a qu'une vésicule de Poli, mais les corps sigmoides sont disposés en amas et les urnes ciliées bien différentes.

REMARQUES SUR LA CLASSIFICATION DES DENDROCHIROTES PAR PANNING, 1949.

La très intéressante tentative de Panning d'une classification des Dendrochirotes, est malheureusement viciée à la base du fait que l'auteur n'a pas pu examiner tous les échantillons dont il parle et a dû travailler sur fiches. De très nombreuses erreurs ont été commises, les descriptions des auteurs étant souvent insuffisantes pour permettre une rigoureuse détermination des genres. Je n'ai donc pas tenu compte, dans ce travail, de la classification de Panning, bien que de nombreuses observations soient à retenir. A titre indicatif, je donne ci-dessous, avec l'indication de la pagination, la position générique de quelques espèces d'Afrique du Sud, telle que la conçoit Panning.

Stereoderma jägeri (Lampert), p. 422.
Pseudocnus leoninus var. *africanus* (Britten), p. 422.
Pseudocnus sykion (Lampert), p. 422.
Trachythyone crucifera (Semper), p. 426.
Ludwigia spyridophora (H. L. Clark), p. 431.
Ludwigia tetracentriophora (Heding), p. 431.
Ocnus capensis (Théel), p. 437.
Ocnus insolens (Théel), p. 437.
Colochirus doliolum (Pallas), p. 439.
Havelockia venustella (Ludwig et Heding), p. 466.

En ce qui concerne *Stereoderma jägeri*, Panning donne la description d'un échantillon du Musée de Hambourg, récolté en 1928 à Zanzibar, étiqueté par erreur *Pseudocucumis africana*, et qu'il rapporte, avec réserves, à *Cucumaria jägeri* Lampert. Je ne pense pas que cette identification soit

exacte. En effet, le type de Lampert a les pieds du trivium disposés sur trois–quatre rangées dans chaque radius, les pieds du bivium en trois–quatre rangées, alors que l'échantillon étudié par Panning a les pieds ventraux simplement bisériés et ceux du bivium très dispersés sur la surface dorsale. La forme des couronnes calcaires ne semble pas correspondre. *C. jägeri* a une vésicule de Poli, alors que l'exemplaire de Panning en a deux. Enfin, Lampert parle de spicules très massifs et épais garnis de nodules, alors que Panning ne trouve que des plaques très isolées pourvues de protubérances. Il est très dommage que Panning n'ait pas figuré ces plaques, ce qui aurait grandement servi à identifier son échantillon.

ADDITIF

L'étude des Holothuries de l'Afrique du Sud était terminée et le manuscrit envoyé pour impression, lorsque je reçus de M. le Professeur Day un lot de douze Holothuries récoltées dans la Baie de Durban et dans la Baie de Langebaan, de juillet 1950 à mai 1951. Ces douze Holothuries appartiennent aux espèces suivantes: ***Holothuria parva*** Lampert, ***Holothuria scabra*** Jaeger, ***Pentacta doliolum*** (Pallas), ***Thyone aurea*** (Quoy et Gaimard), ***Taeniogyrus Dayi*** Cherbonnier. Les trois dernières espèces ont été étudiées en détail dans la première partie de ce mémoire, et je me contenterai d'indiquer ci-dessous leur provenance exacte. Par contre, j'estime qu'il y a lieu de consacrer une étude approfondie à ***Holothuria parva*** et à ***Holothuria scabra***: la première, parce-qu'assez mal connue quant à son anatomie, la forme de la couronne calcaire et celle des spicules; la seconde, parce-que nouvelle pour les côtes sud-africaines.

Pentacta doliolum (Pallas)

Université de Cape Town: LB. 282Z, le 4–V–1951, 2 ex. pourpres récoltés à l'Ile Skaapen (côté lagoon); côte rocheuse, plus bas que la zone à Balanes et bordure sublittorale, au niveau des basses-eaux de printemps.—LB. 317N, 1 ex.

Thyone aurea (Quoy et Gaimard)

LB. 310J, le 5–V–1951, 1 ex. dragué dans le sable au milieu du canal.—LB. 318N, 1 ex.

Taeniogyrus Dayi Cherbonnier

LB. 310K, 4 ex. de couleur pourpre dragués dans le sable, au milieu du canal, le 5–V–1951.

Holothuria parva Lampert

Pl. *49*, figs. 1–23.

Holothuria parva Lampert, 1885, p. 246, pl. i, fig. 38.
Holothuria lubrica Selenka var. *parva* Krauss, Panning, 1934, 2. Teil. p. 45, Abb. 39 (synonymie complète).
Halodeima parva Heding, 1940, p. 120.
Holothuria parva Deichmann, 1948, p. 339, pl. xvii, figs. 22–27.

Spécimen étudié.

Université de Cape Town: DBN. 20A, Baie de Durban, 1 ex. noirâtre récolté le 12–VII–1950 parmi les racines de Palétuviers, à moitié enfoui dans le sable vaseux.

L'unique exemplaire mesure 77 mm. de long sur 30 mm. de large. Il est de forme subcylindrique, à tentacules invaginés. Sa couleur est uniformément marron noir. Très contracté, il est profondément plissé transversalement. Le tégument est épais, lisse.

Bouche et anus terminaux. Vingt petits tentacules noirâtres, de taille égale. Pieds ventraux relativement nombreux, disposés sans ordre sur les radius et les interradius; ils sont très longs, à tige cylindrique translucide, à extrémité renflée de couleur Terre de Sienne, terminée par une large ventouse blanchâtre soutenue par un très grand disque calcaire. Pieds dorsaux plus rares que les ventraux, courts, cylindriques, à ventouse soutenue par un disque calcaire légèrement plus petit que celui des pieds ventraux.

Couronne calcaire bien calcifiée (*49*, 22); les radiales sont hautes, fortement échancrées à la partie antérieure; les interradiales sont triangulaires. Ampoules tentaculaires assez longues, pignentées de brun. Deux longues Vésicules de Poli, pigmentées comme les ampoules tentaculaires. Un court canal hydrophore à madréporite allongé peu calcifié, le tout situé dans le mésentère dorsal. Gonades formées d'une trentaine de longs tubes blanchâtres plusieurs fois ramifiés. Poumon gauche atteignant la longueur du corps, très ramifié; poumon droit atrophié. Quelques tubes de Cuvier, jaunâtres. Vaste cloaque. Muscles longitudinaux très larges, bifides, épais, à bords libres. Vésicules pédieuses bien développées. Anus sans dents.

Spicules.—Les spicules du tégument ventral et du tégument dorsal ne sont pas identiques. Ceux du tégument ventral se composent surtout de bâtonnets massifs, sans aspérités (*49*, 1) ou portant d'assez nombreuses épines réparties sur les bords et sur le corps du spicule (*49*, 2, 3); d'autres bâtonnets sont plus élancés, à surface lisse (*49*, 6) ou dont les bords sont fortement denticulés avec le corps portant quelques forts piquants (*49*, 4, 7).

Les bâtonnets du tégument dorsal sont moins massifs, à épines marginales

plus développées (*49*, 8, 9, 10, 11); on rencontre également, et en grande quantité, des bâtonnets à épines marginales encore plus fortes, à épines médianes aussi fortes que les marginales (*49*, 12, 16, 18, 19); de nombreuses plaques, plusieurs fois perforées, se trouvent au voisinage de la base des pieds (*49*, 17, 21).

Les parois pédieuses sont absolument dépourvues de spicules, sauf celles des pieds de la région entourant l'anus, qui sont soutenues par de petites baguettes (*49*, 14, 20) et de longs bâtonnets larges, à bords fortement échancrés et plusieurs fois perforés (*49*, 23).

Les tentacules sont renforcés par des bâtonnets grêles, à bords très ondulés, à surface fortement noduleuse (*49*, 5) et par des bâtonnets plus longs et plus larges, ne portant que quelques fines épines aux extrémités (*49*, 15).

Enfin, dans la région anale, on rencontre quelques tourelles, malheureusement en voie de décalcification, dont la flèche est formée de quatre piliers assez hauts, grêles (*49*, 13); ces tourelles, quoique mal conservées, sont certainement celles que Miss Deichmann signale n'avoir trouvées que chez le très petit exemplaire de *H. parva*, étudié par elle, et provenant de Port-Edward.

Le type Lampert provient de Natal et d'autres exemplaires de cette espèce ont été récoltés de Zanzibar à Port-Edward, ainsi que dans le Golfe Persique.

Holothuria scabra Jaeger

Pl. *50*, figs. 1–20.

Holothuria scabra **Jaeger, 1833, p. 23.—Panning, 1935, p. 80, Abb. 66 (synonymie complète).**

Holothuria tigris **Selenka, 1867, p. 333, pl. xix, figs. 70–72.**

Spécimens étudiés.

Université de Cape Town: DBN 34E, deux exemplaires noirs, mouchetés, récoltés le 16–VII–1950 dans la baie de Durban, à demi enfouis dans le sable liquide; espèce très commune, atteignant une longueur de neuf pouces, et que l'on trouve au-dessous du niveau des basses-eaux de printemps.

Les deux exemplaires, qui sont partiellement éviscérés, sont fortement contractés, plissés transversalement et il est impossible de constater la répartition des pieds et des papilles. Ces échantillons sont aplatis ventralement et mesurent respectivement 55 mm. et 77 mm. de long, 42 et 47 mm. de large et 21 et 36 mm. de hauteur. Les tentacules sont invaginés. La partie dorsale est gris noirâtre alors que la partie ventrale est gris clair, ponctuée de nombreuses petites taches noires.

Bouche ventrale, anus terminal. Tégument très épais. Dix-huit petits tentacules noirâtres, de taille égale. Couronne calcaire peu calcifiée, à

radiales hautes dont la partie antérieure est profondément encochée, à interradiales triangulaires (*50*, 10). Ampoules tentaculaires bien développées. Une très longue vésicule de Poli. Un long canal hydrophore tortillonné dans le mésentère dorsal et terminé par un petit madréporite en forme de doigt.

Pieds ventraux assez nombreux, longs, cylindriques, terminés par une large ventouse soutenue par un grand disque calcaire très réticulé. Papilles dorsales peu nombreuses, assez longues, coniques, à tige blanchâtre, dépourvues de disque calcaire.

Muscles longitudinaux très puissants, épais, bifides, à bords libres. Gonades formées d'un très grand nombre de tubes très fins, ramifiés. Poumons très développés. Vaste cloaque. Anus sans dents.

Spicules.—Les spicules du tégument se composent de boutons et de tourelles, ces dernières identiques dans le trivium et le bivium.

Les boutons du tégument ventral sont généralement à six trous, à bords plus ou moins ondulés, à surface portant soit des esquisses de nodules (*50*, 1, 3), soit le plus souvent deux gros nodules centraux (*50*, 2); certains de ces boutons, plus grands, ont de dix à vingt perforations (*50*, 4).

Les boutons du tégument dorsal, le plus souvent à six trous, sont bien plus noduleux (*50*, 8, 9); on en rencontre qui ont de huit à dix trous (*50*, 7).

Le disque des tourelles, à bord ondulé, est percé le plus souvent d'un trou central plus ou moins grand et de douze–trente trous de taille inégale (*50*, 11, 13, 14, 17); la flèche, à quatre piliers, est peu haute, massive (*50*, 12, 15) et se termine par une couronne, percée en son centre d'un large trou, à bord portant de dix–quinze épines, et armée de plusieurs épines sub-latérales (*50*, 14, 17); certaines tourelles, à disque plus grand, plus réticulé, ont une flèche dont la couronne a une structure plus compliquée (*50*, 13). Enfin, des tourelles, plus rares, ont le disque subrectangulaire fortement ondulé et la couronne porte des épines bien plus prononcées (*50*, 16).

Les bâtonnets des pieds ventraux et des papilles dorsales sont identiques (*50*, 5, 6); ceux des tentacules, perforés ou non aux extrémités, sont très fortement épineux (*50*, 18, 20).

Rapports et différences.—Le type de *H. scabra* a été récolté aux Célèbes, mais la présence de l'espèce a été signalée depuis les Iles Fidji et Carolines jusqu'aux côtes est d'Afrique, notamment à Zanzibar. Il n'est donc pas étonnant de la retrouver à Durban, où elle n'avait jamais été signalée, bien qu'elle y soit commune.

Au point de vue aspect et coloration, mes échantillons ressemblent exactement à l'exemplaire de *H. tigris* figuré par Selenka et non pas à celui de *H. scabra*, figuré par Semper. L'organisation interne est bien comme figurée et décrite par Selenka pour *H. tigris* mais les spicules (boutons) de

cette dernière espèce sont sans nodules, sans doute par suite d'une mauvaise observation de Selenka. J'ai pu, par ailleurs, comparer les exemplaires de Durban avec quelques *H. scabra* des Iles Andaman et d'Océanie; je n'ai relevé que de très légères différences de coloration alors que les spicules sont absolument identiques.

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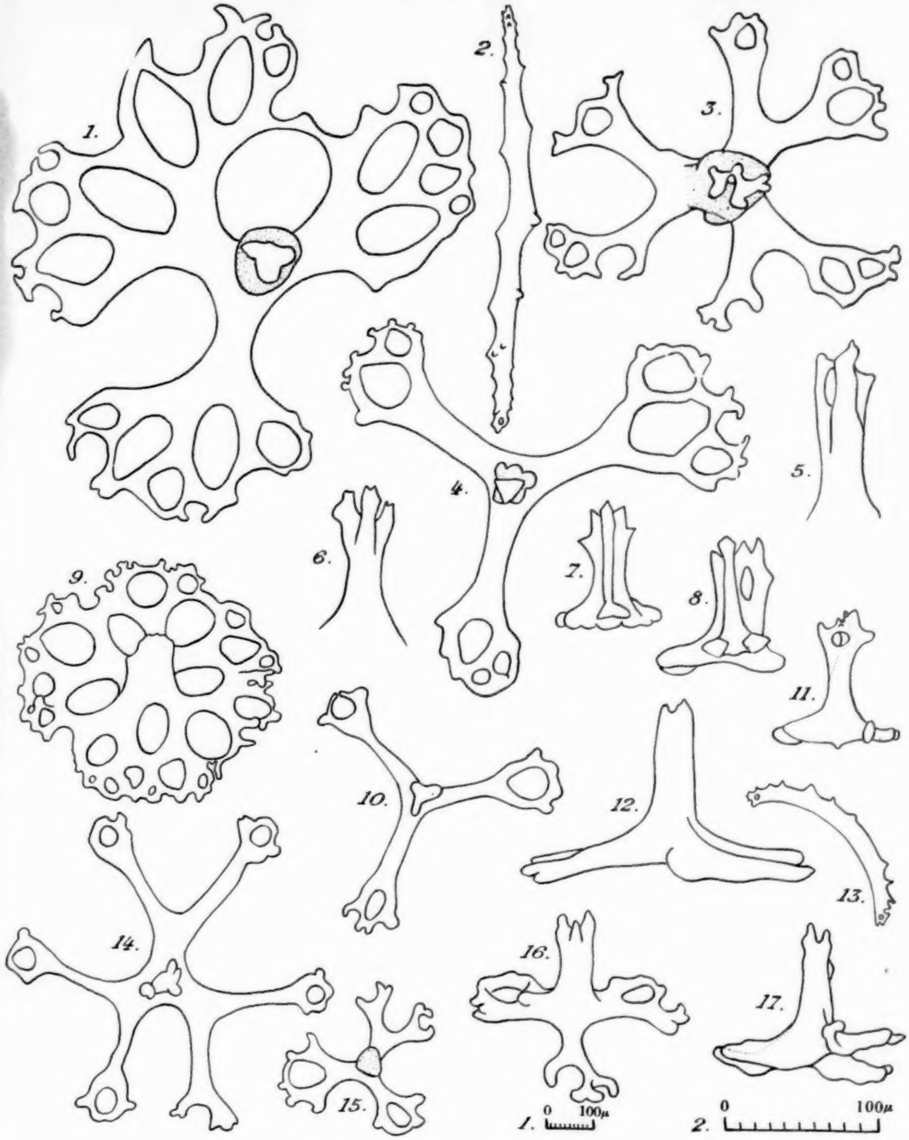

PLANCHE 35.

Figs. 2, 13, éch. 1; autres figs., éch. 2.

Synallactes viridilimus n. sp.

Figs. 1, 3, 4.—Très grandes tourelles du tégument dorsal.
Figs. 2, 9, 13.—Bâtonnets des tentacules.
Figs. 5, 6.—Flèches des grandes tourelles du tégument dorsal.
Figs. 7, 8, 11.—Petites tourelles du tégument.
Figs. 10, 14.—Tourelles grêles du tégument dorsal.
Figs. 12, 15–17.—Grandes tourelles du tégument.

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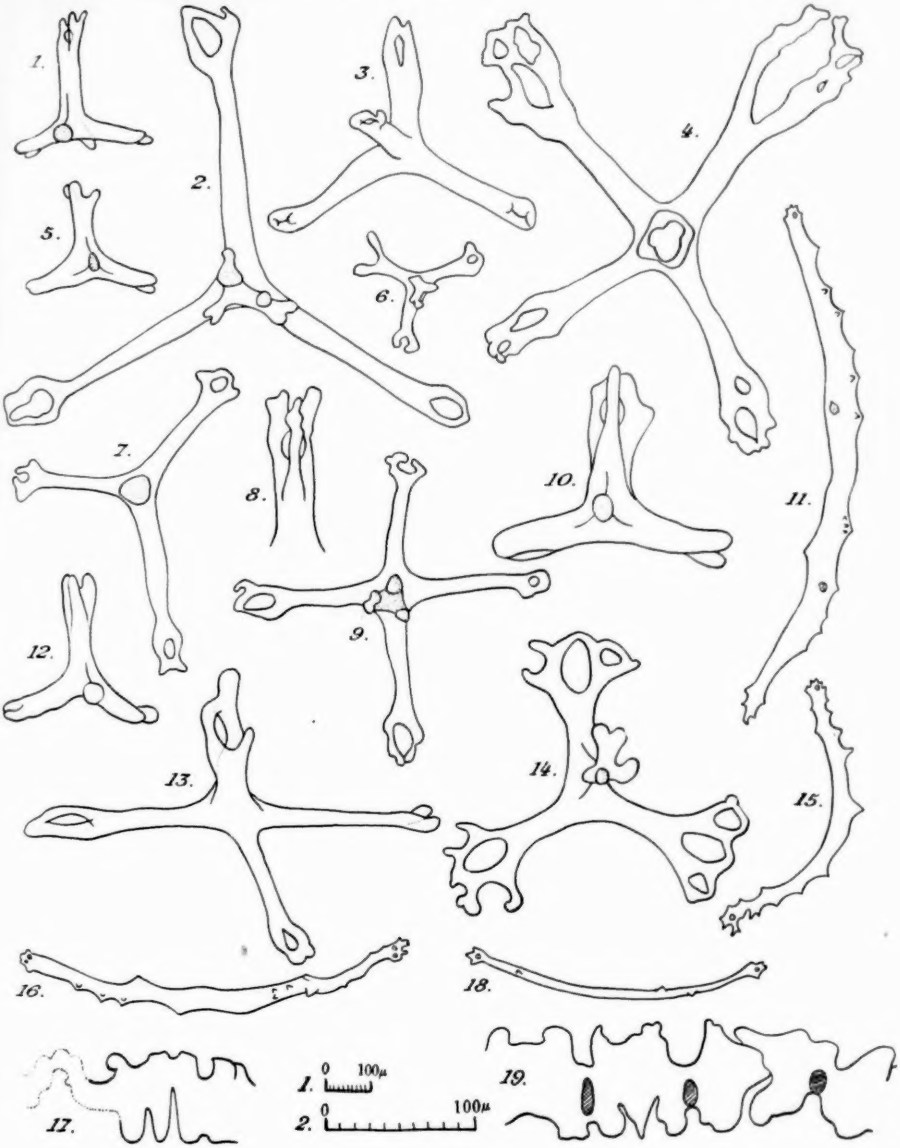

Planche 36.

Figs. 11, 15, 16, 18, éch. 1; figs. 17, 19, ×4 environ; autres figs., éch. 2.

Synallactes mollis n. sp.

Figs. 1, 5, 6, 12.—Petites tourelles du tégument ventral. Figs. 2, 4, 7, 9, 1 irandes tourelles du tégumen d.
Figs. 3, 10, 13.—Grandes tourelles du tégument ventral. Fig. 8.—Flèche randes tourelles du tegument v l.
Figs. 11, 15.—Bâtonnets des tenta ules. Fig. 18.—Bâtonnets des pieds ux.
Fig. 19.—Couronne calcaire ×4 environ.

Synallactes viridilimus n. sp.

Fig. 16.—Bâtonnets des pie ventraux. Fig. 17.—Couronne calcaire ×4 environ.

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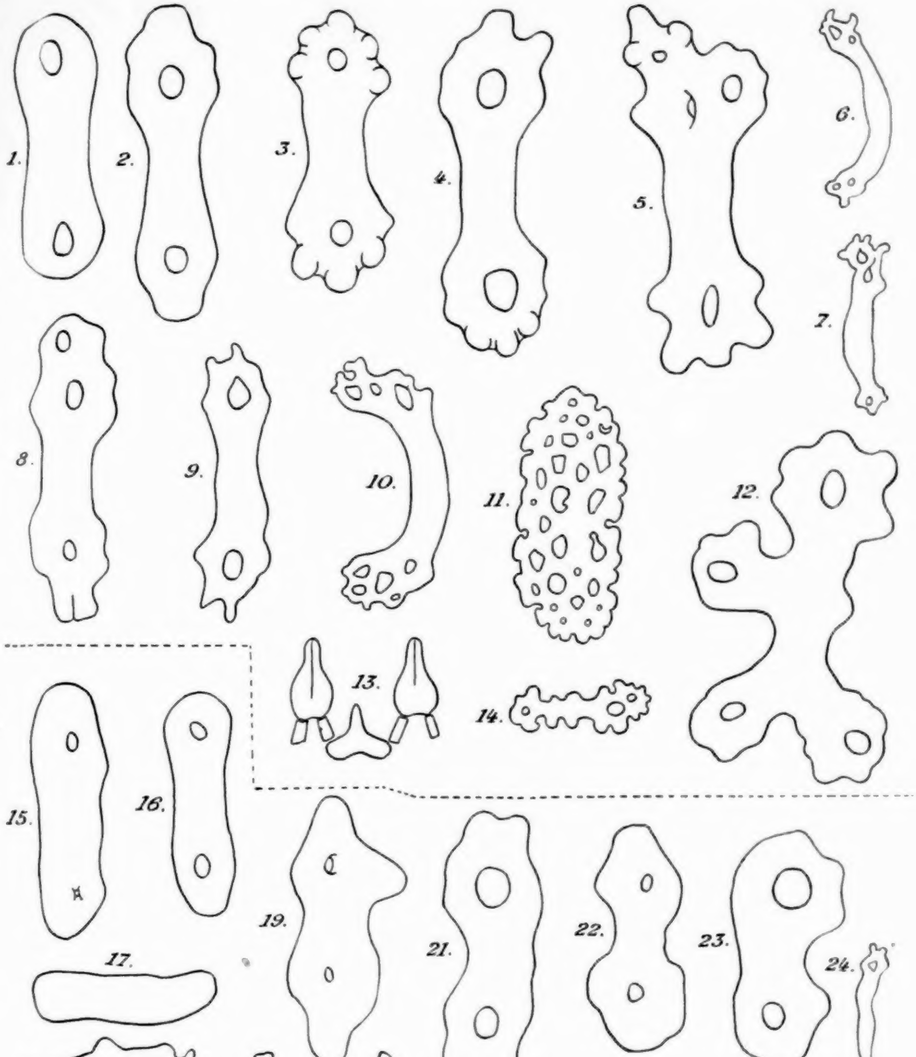

PLANCHE 37.

Cucumaria frauenfeldi Ludwig

Figs. 1–5, 8, 9, 12.—" Biscuits " du tégument.
Figs. 6, 7, 10.—Bâtonnets des pieds.
Figs. 11, 14.—Corpuscules crépus des tentacules.
Fig. 13.—Couronne calcaire ×8 environ.

Cucumaria deichmanni n. sp.

Figs. 15–17, 19, 21–23.—" Biscuits " du tégument.
Figs. 18, 20, 24.—Bâtonnets des pieds.

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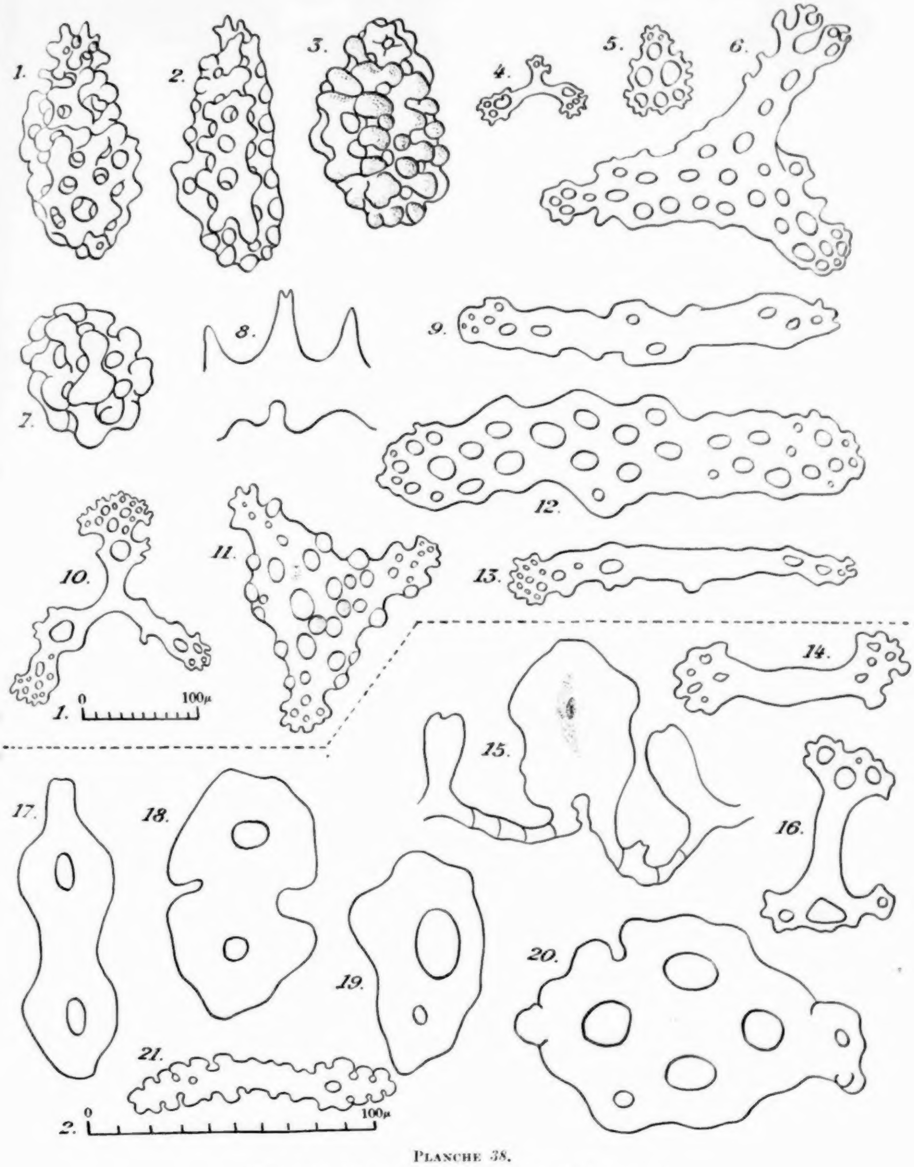

PLANCHE 38.

Figs. 1–13, éch. 1; figs. 14–21, éch. 2; figs. 8, 15, × 8.

Cucumaria sinorbis n. sp.

Figs. 1–3, 7.—Gros spicules du tégument. Figs. 4, 10, 11, 13.—Bâtonnets et plaques des pieds. Figs. 5, 6, 9, 12.—Bâtonnets et plaques des tentacules. Fig. 8.—Couronne calcaire ×8 environ.

Cucumaria deichmanni n. sp.

Figs. 14, 16.—Bâtonnets des pieds. Fig. 15.—Couronne calcaire 8 environ.
Fig. 17.—"Biscuits" du tégument. Figs. 18–20.—Plaques lisses tégument dorsal.
Fig. 21.—Corpuscule crépu des tentacules.

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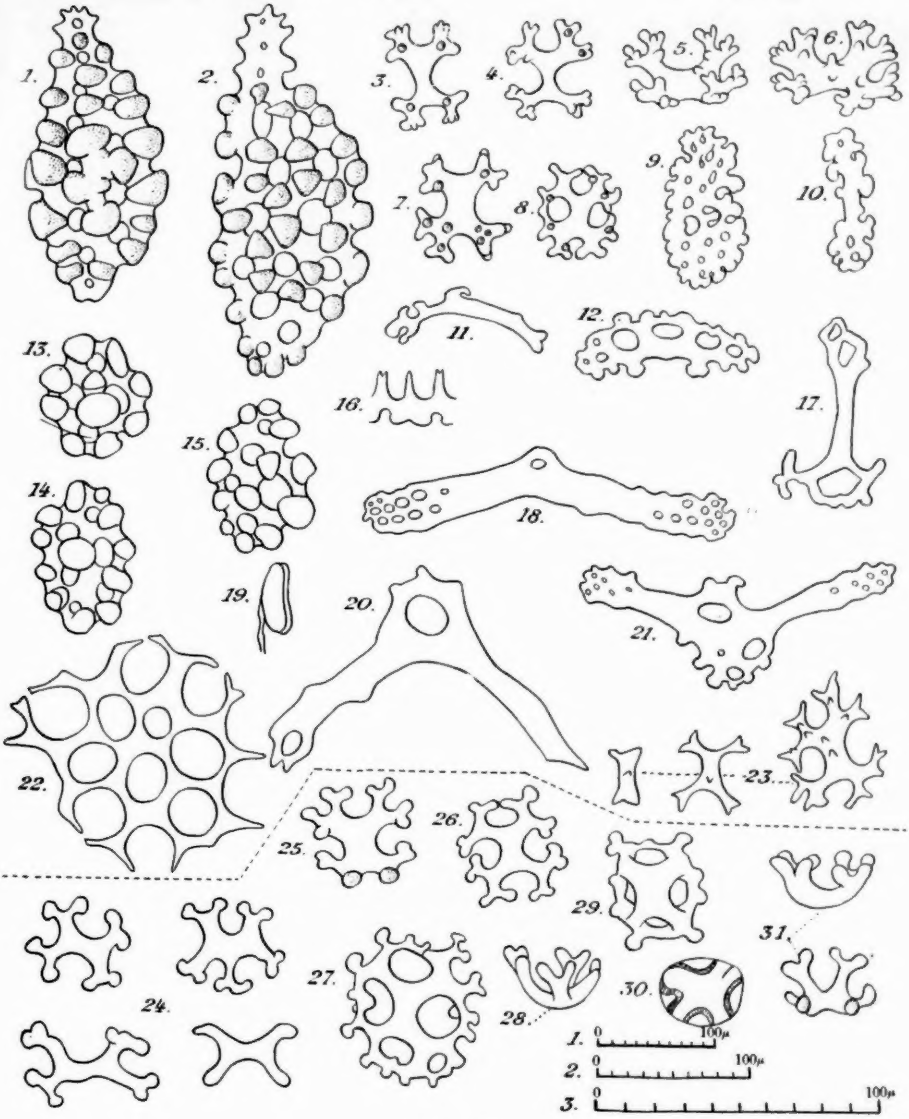

PLANCHE 39.

Figs. 18, 20, 21, éch. 1; figs. 1, 2, 13–15, 22, éch. 2; figs. 16, 19, 30, ×8 environ; autres figs., éch. 3.

Cucumaria insolens Théel

Figs. 1, 2.—Gros spicules du tégument. Figs. 3–8.—Corbeilles du tégument.
Figs. 9–12.—Corpuscules crépus des tentacules. Figs. 13–15.—Boutons du tégument.
Fig. 16.—Couronne calcaire ×8 environ. Figs. 17, 18.—Bâtonnets des tentacules.
Fig. 19.—Madréporite ×8 environ. Fig. 20.—Bâtonnets des tentacules des embryons.
Fig. 21.—Bâtonnets des pieds. Fig. 22.—Plaque à larges mailles du tégument des embryons.
Fig. 23.—Corbeilles du tégument des embryons.

Cucumaria sinorbis n. sp.

Figs. 24–29, 31.—Corbeilles du tégument. Fig. 30.—Madréporite ×8 environ.

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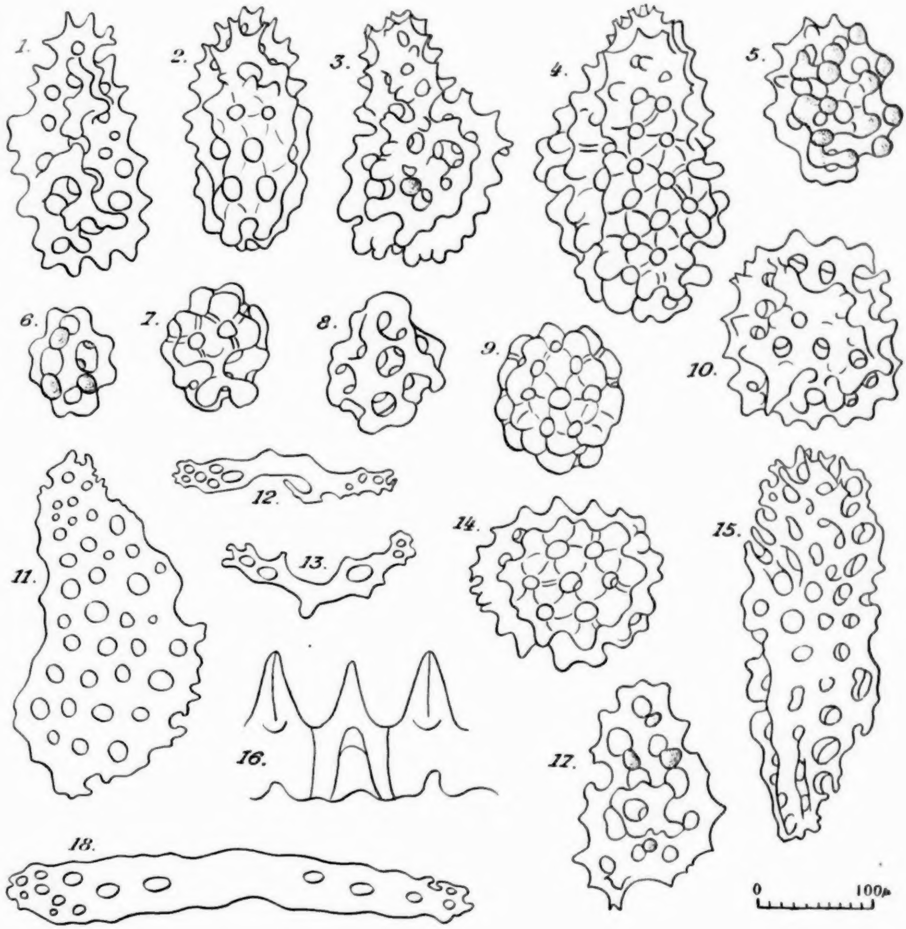

PLANCHE 40.

Cucumaria sykion Lampert

Figs. 1–10, 14, 17.—Gros spicules du tégument.
Fig. 11.—Grande plaque lisse de la région anale.
Figs. 12, 13.—Bâtonnets des pieds.
Fig. 16.—Couronne calcaire ×5 environ.
Figs. 15, 18.—Plaques et bâtonnets des tentacules.

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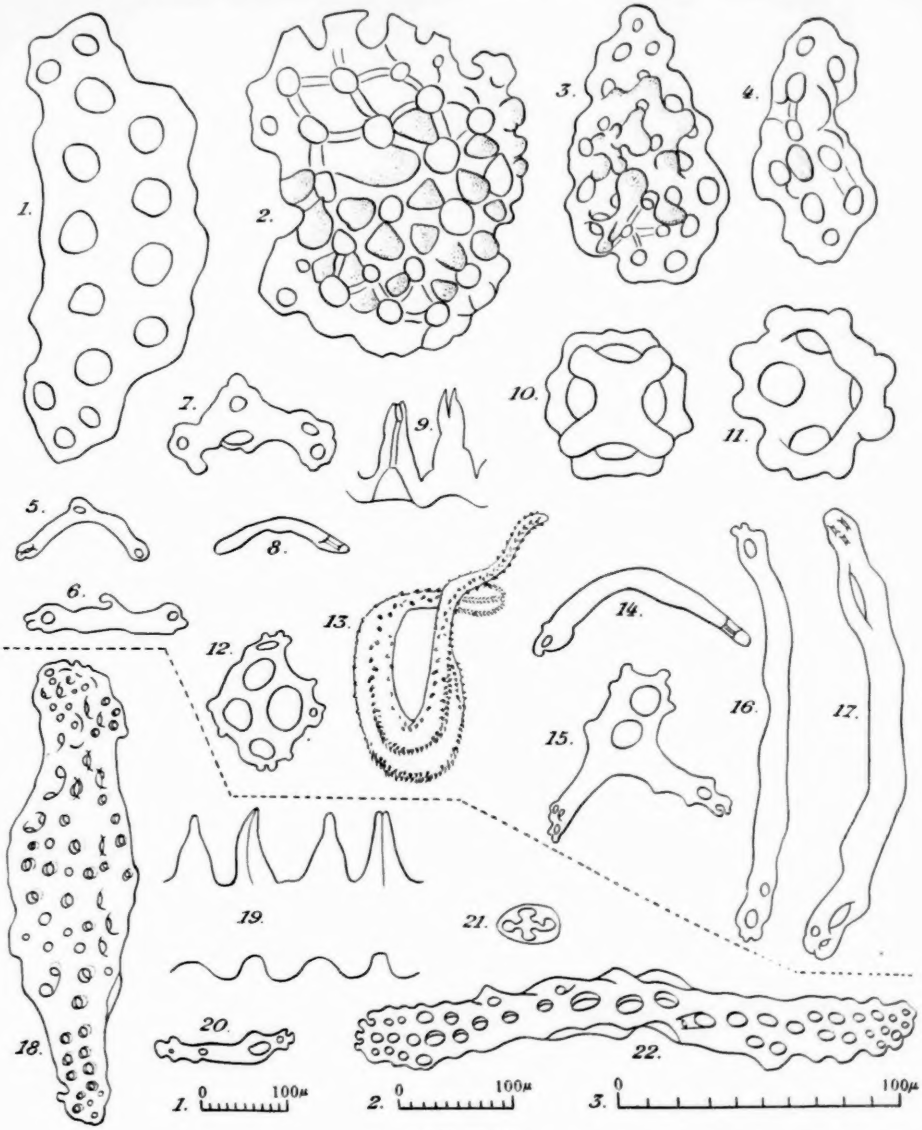

PLANCHE 41.

Figs. 1–8, 14, 16, 17, éch. 1; figs. 18, 20, 22, éch. 2; figs. 10–12, 15, éch. 3; figs. 9, 19, 21, ×5 environ; fig. 13, grandeur nature.

Cucumaria rigidapeda n. sp.

Fig. 1.—Grande plaque lisse de la couche profonde. Figs. 2–4.—Plaques noduleuses de la couche profonde.
Figs. 5–8.—Bâtonnets des papilles. Fig. 9.—Couronne calcaire ×5 environ.
Figs. 10, 11.—Corbeilles du tégument. Figs. 12, 14–17.—Bâtonnets et coupes des tentacules.
Fig. 13.—Echantillon type figuré grandeur nature.

Cucumaria tetracentriophora Heding

Figs. 18, 20, 22.—Bâtonnets des tentacules. Fig. 19.—Couronne calcaire ×5 environ.
Fig. 21.—Madréporite ×5 environ.

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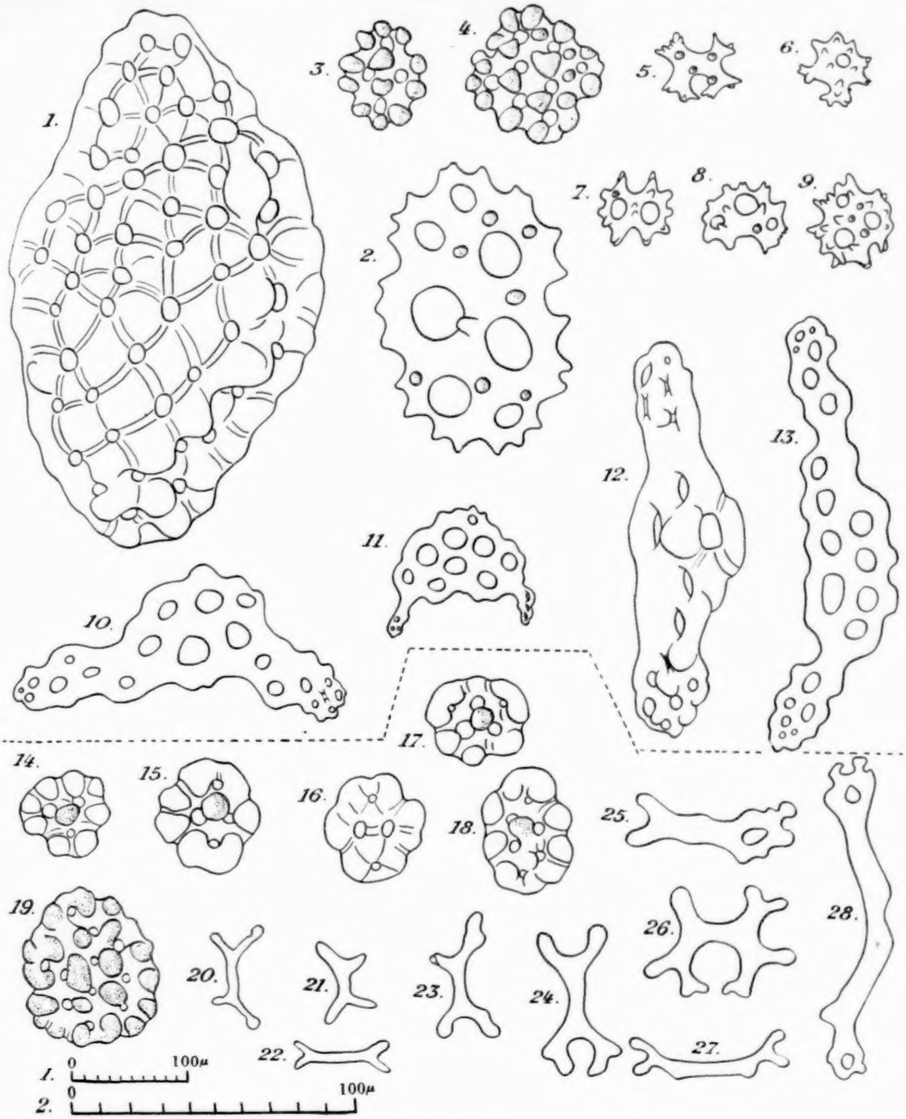

PLANCHE 42.

Figs. 1, 3, 4, 10, 11–19, éch. 1; autres figs., éch. 2.

Cucumaria capensis Théel

Fig. 1.—Enorme spicule du tégument. Fig. 2.—Plaque denticulée de la région anale. Figs. 3, 4.—Boutons du tégument. Figs. 5–9.—Corbeilles du tégument. Figs. 10, 11.—Bâtonnets et plaques des tentacules. Figs. 12, 13.—Bâtonnets des pieds.

Cucumaria tetracentriophora Heding

Figs. 14–19.—Boutons du tégument. Figs. 20–28.—Bâtonnets du tégument.

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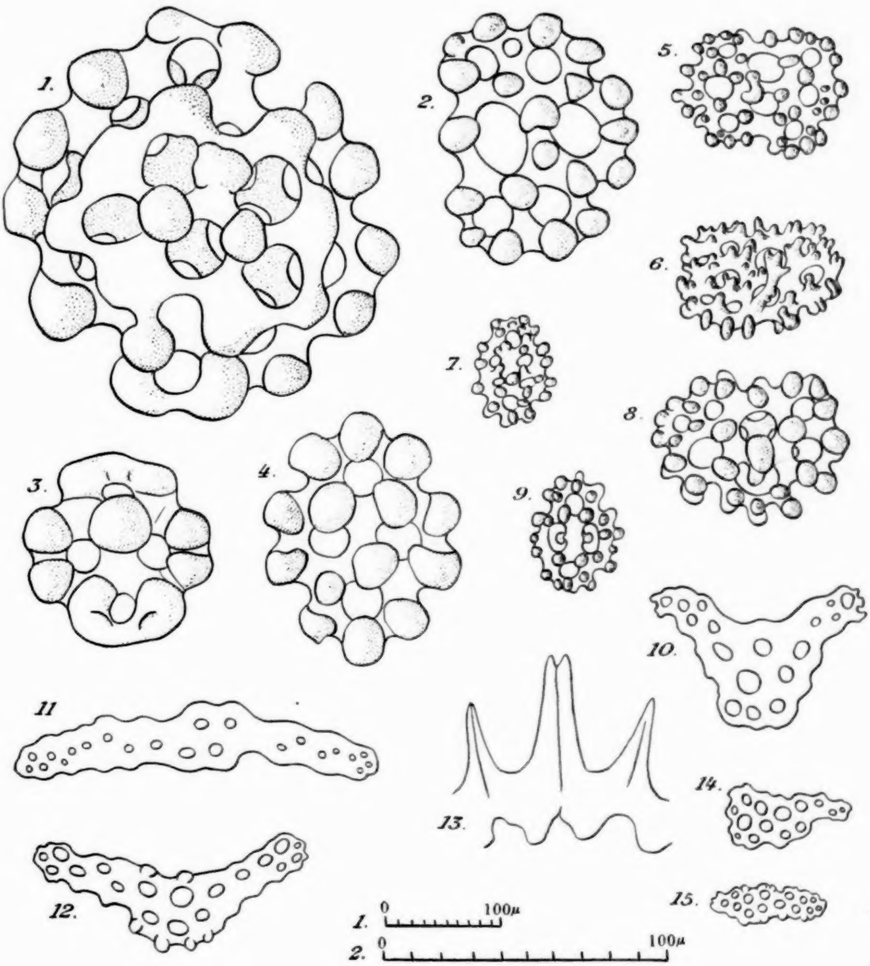

PLANCHE 43.

Figs. 10–12, 14, 15, éch. 1; figs. 1–9, éch. 2; fig. 13, ×8 environ.

Pentacta doliolum (Pallas)

Figs. 1–4.—Gros boutons du tégument.
Figs. 5–9.—Petits boutons du tégument.
Figs. 10, 12.—Bâtonnets des pieds.
Figs. 11, 14, 15.—Bâtonnets et plaques des tentacules.
Fig. 13.—Couronne calcaire ×8 environ.

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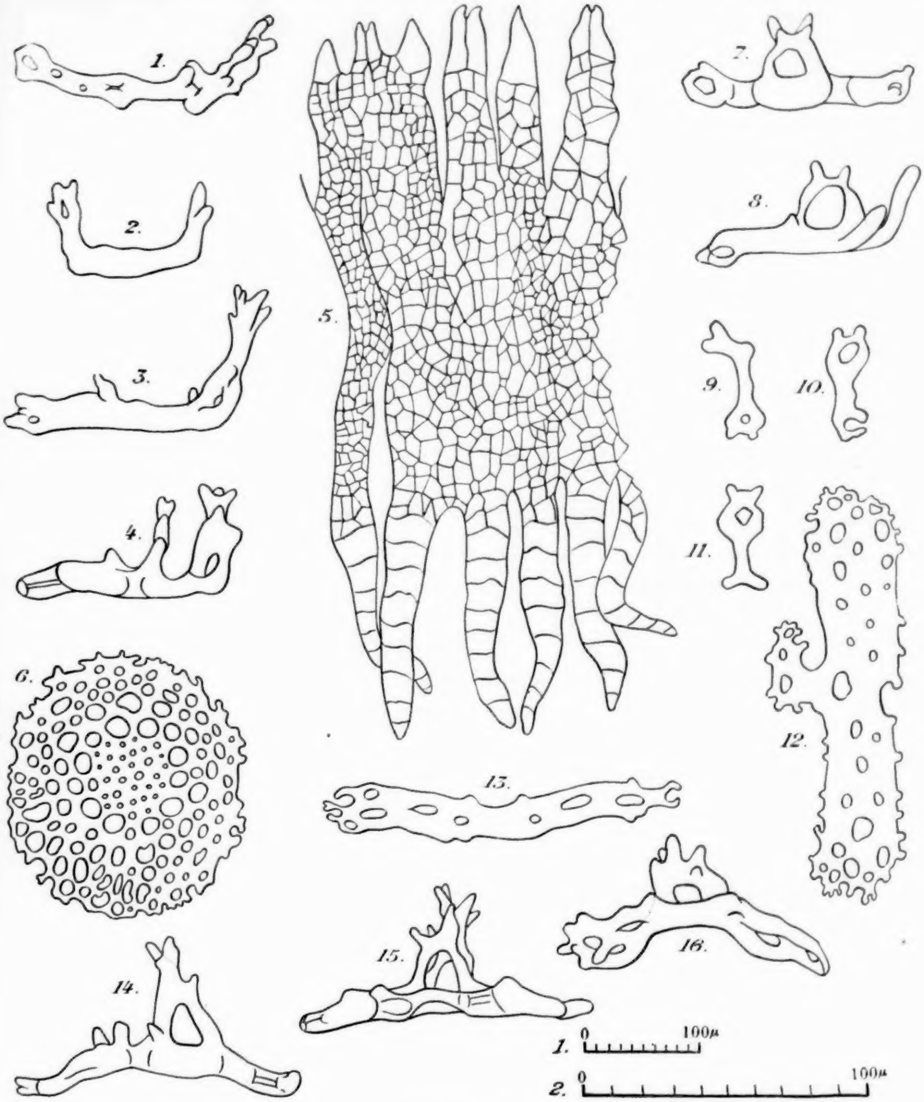

PLANCHE 44.

Figs. 6, 12, 13, éch. 1; fig. 5, × 8 environ; autres figs., éch. 2.

Thyone proceracorona n. sp.

Figs. 1–4.—Spicules des pieds et aussi du tégument.
Fig. 5.—Couronne calcaire × 8 environ.
Fig. 6.—Disque terminal calcaire des pieds.
Figs. 9–11.—Petits spicules du tégument.
Figs. 12, 13.—Bâtonnets des tentacules.

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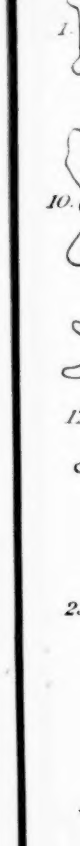

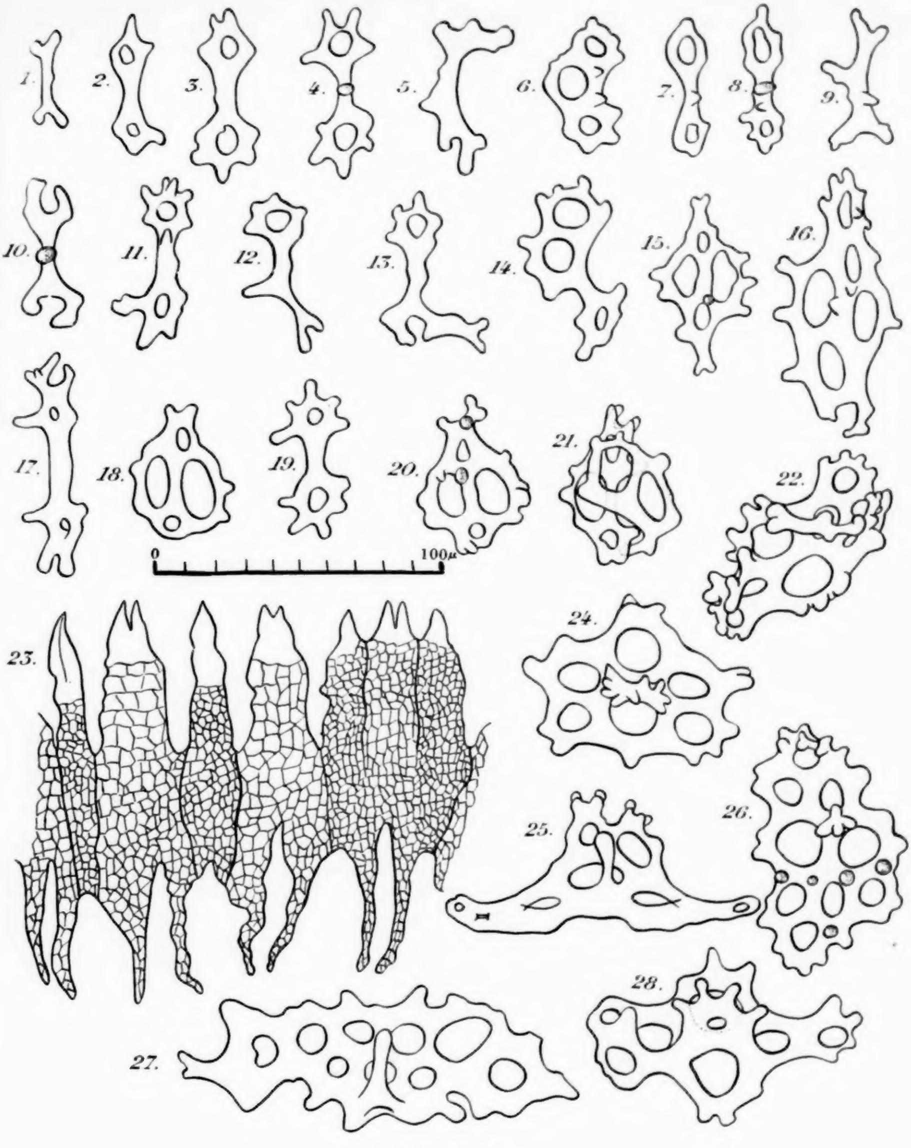

PLANCHE 45.

Thyone aurea (Quoy et Gaimard)

Figs. 1–3, 9, 10, 17, 19.—Bâtonnets du tégument ventral.
Figs. 4, 7, 8, 11–13.—Bâtonnets du tégument dorsal.
Figs. 5, 6, 14, 15, 18, 20, 27.—Plaques du tégument dorsal.
Figs. 16, 22.—Plaques losangiques de la région anale.
Fig. 21.—Coupe irrégulière du tégument.
Fig. 23.—Couronne calcaire ×3, 5 environ.
Figs. 24–26, 28.—Tourelles de la région anale.

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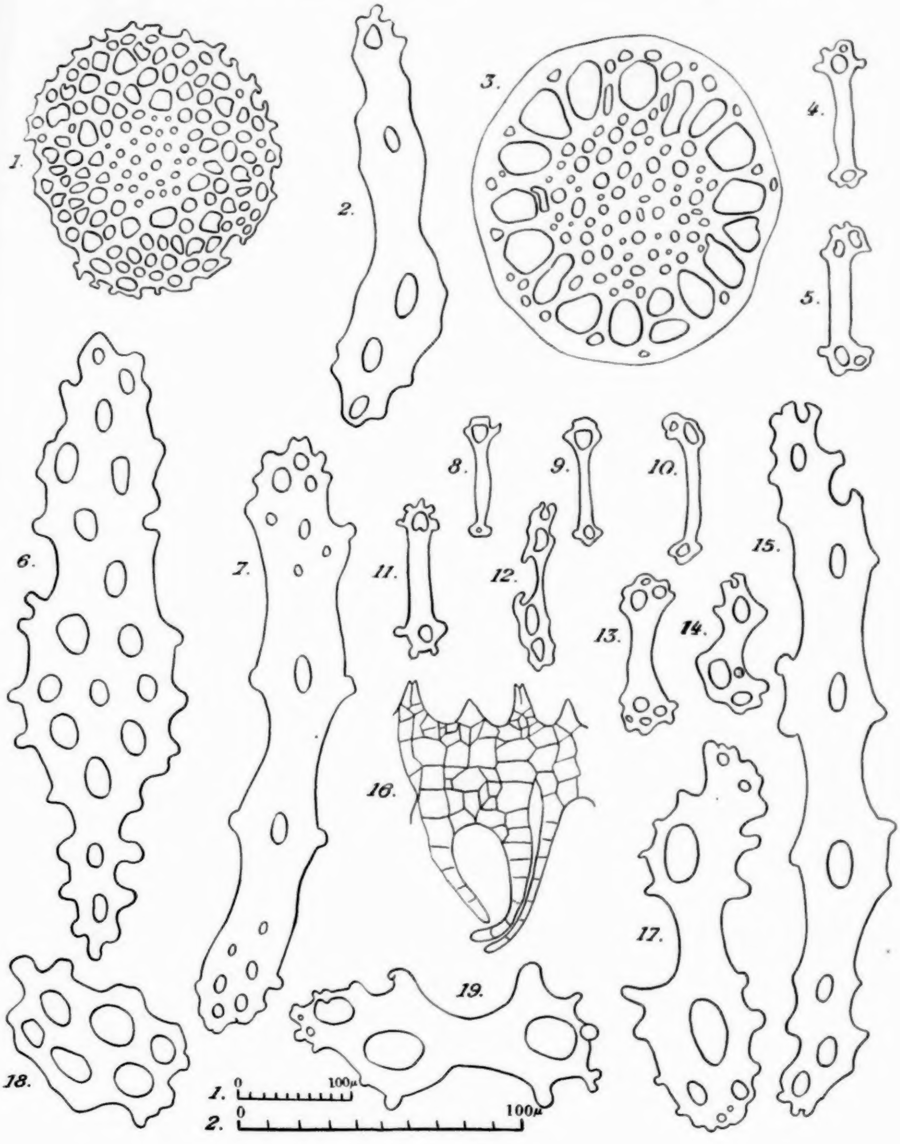

PLANCHE 46.

Fig. 1, éch. 1; fig. 16, × 7 environ; autres figs. éch. 2.

Thyone aurea (Quoy et Gaimard)

Fig. 1.—Disque terminal calcaire des pieds. Figs. 2, 6, 7.—Bâtonnets des tentacules.

Thyone articulata Vaney

Fig. 3.—Disque terminal calcaire des pieds. Figs. 4, 5, 8–13.—Bâtonnets du tégument.
Figs. 14, 18.—Plaques de la région anale. Figs. 15, 17, 19.—Bâtonnets des tentacules.
Fig. 16.—Couronne calcaire × 7 environ.

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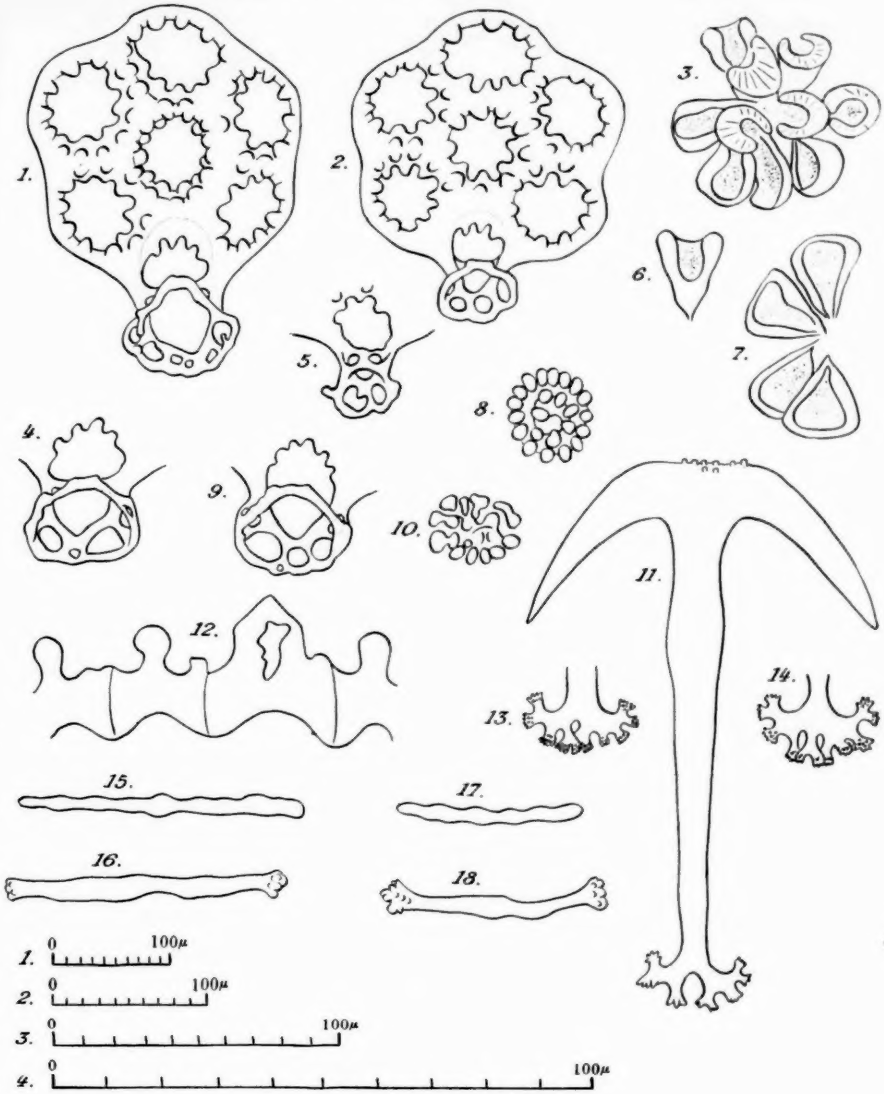

PLANCHE 47.

Figs. 3, 6, 7, éch. 1; figs. 1, 2, 4, 5, 9, 11, 13, 14, éch. 2; figs. 15-18, éch. 3; figs. 8, 10, éch. 4; fig. 12, × 7 environ.

Opheodesoma mauritiae Heding

Fig. 1.—Plaque anchorale de la région moyenne. Fig. 2.—Plaque anchorale de la région orale.
Figs. 3, 6, 7.—Urnes ciliées des mésentères. Figs. 4, 9.—Partie basilaire d'une plaque anchorale de la région moyenne.
Fig. 5.—Partie basilaire d'une plaque anchorale de la région orale. Figs. 8, 10.—Granules miliaires du tégument.
Fig. 11.—Ancre. Fig. 12.—Couronne calcaire × 7 environ.
Figs. 13, 14.—Parties basilaires des ancres. Figs. 15-18.—Bâtonnets des tentacules.

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PLANCHE 48.

Tæniogyrus dayi n. sp.

Fig. 1.—Roue vue du dessus. Fig. 2.—Roue vue légèrement de profil.
Figs. 3, 4.—Corps sigmoides des muscles longitudinaux. Fig. 5.—Couronne calcaire × 40 environ.
Fig. 6.—Bâtonnets des tentacules, en place. Fig. 7.—Urnes ciliées × 120 environ.

Epitomapta knysnaensis n. sp.

Fig. 8.—Ancre et plaque de grande taille. Fig. 9.—Couronne calcaire × 80 environ.
Fig. 10.—Plaque anchorale. Fig. 11.—Bâtonnets des bandes radiales.
Fig. 12.—Urnes ciliées × 80 environ. Figs. 13, 14.—Bâtonnets des tentacules.

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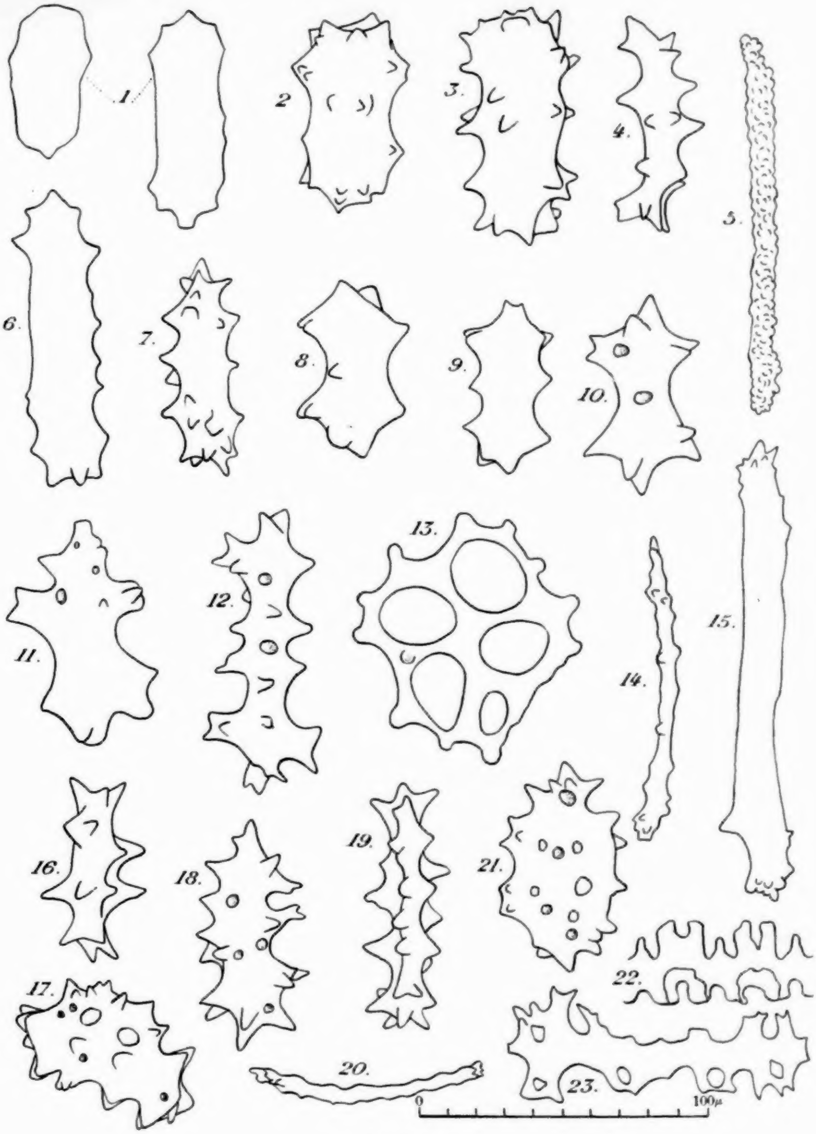

PLANCHE 49.

Holothuria parva Lampert

Figs. 1–7.—Spicules du tégument ventral.
Figs. 5, 15.—Bâtonnets des tentacules.
Figs. 8–12, 16–19, 21.—Spicules du tégument dorsal.
Fig. 13.—Tourelle de la région anale.
Figs. 14, 20, 23.—Bâtonnets des pieds de la région anale.
Fig. 22.—Couronne calcaire ×3 environ.

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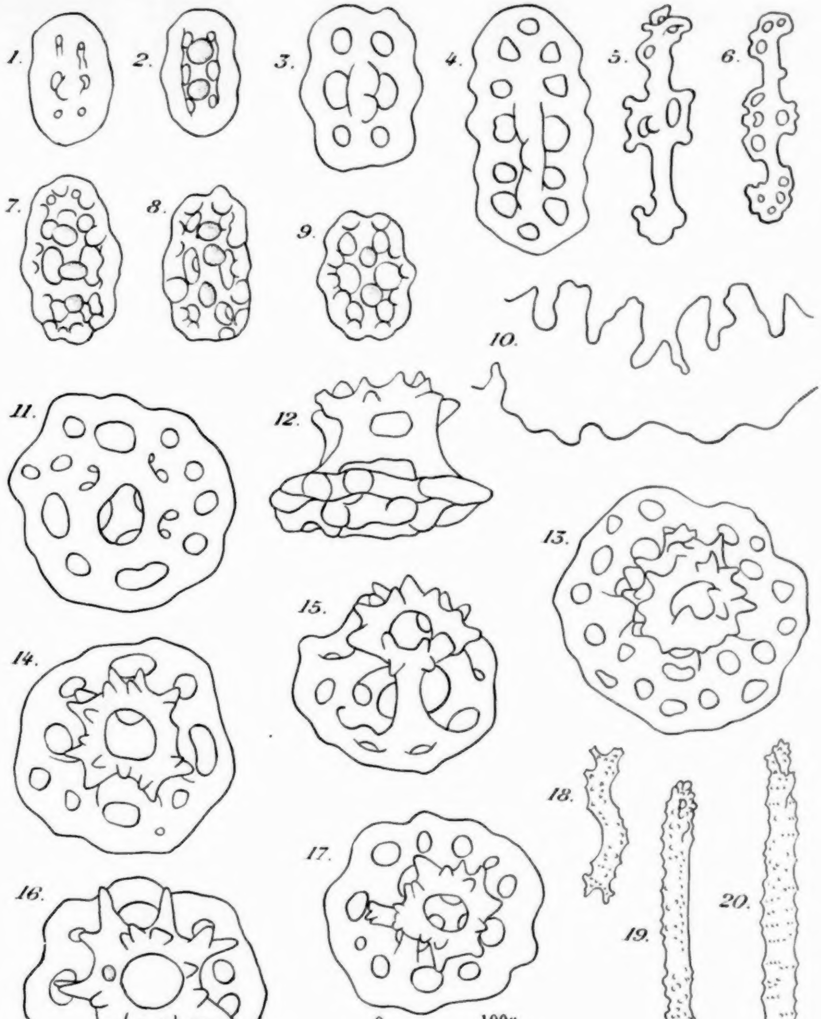

Planche 50.

Figs. 5–6, 18–20, éch. 1; figs. 1–4, 7–9, 11–17, éch. 2; fig. 10, × 8 environ.

Holothuria scabra Jaeger

Figs. 1–4.—Boutons du tégument ventral.
Figs. 5–6.—Bâtonnets des pieds.
Figs. 7–9.—Boutons du tégument dorsal.
Fig. 10.—Couronne calcaire × 8 environ.
Figs. 11–17.—Tourelles du tégument.
Figs. 18–20.—Bâtonnets des tentacu

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